Incidence of the Ascarid *Porrocaecum decipiens* in the Stomachs of Three Species of Seals along the Southern Canadian Atlantic Mainland[1]

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ABSTRACT

Identifications were made of ascarids collected from 1948 to 1956 from the stomachs of 318 harbour seals (*Phoca vitulina*), 812 harp seals (*P. groenlandica*), and 127 grey seals (*Halichoerus grypus*) killed in several localities along the Atlantic coast of Canada. *Porrocaecum* and 2 other genera of ascarids, tentatively identified as *Anisakis* and *Contracaecum*, were present in each species of seal. All 112 male *Porrocaecum* that were identified to species were *P. decipiens*.

Almost all stomachs of harbour and grey seals at all seasons and in all localities contained *P. decipiens*. Considering all localities, the overall average incidence was about 20 adult *P. decipiens* in harbour seals and about 100 in grey seals.

P. decipiens was normally much rarer in the stomachs of harp seals than in the other seals. It appeared most frequently in harp seals taken around the Magdalen Islands in April and May. The incidence of adult *P. decipiens* was much lower during the breeding season of the seals and during their southward and northward migrations within the Gulf of St. Lawrence. The incidence of *P. decipiens* in harp seals from the east coast of Newfoundland was very low.

The relative importance of each species of seal as a vector of *P. decipiens* is as follows. The harbour seal is the most important in the Bay of Fundy and along the southwestern coast of Nova Scotia. Elsewhere harbour and grey seals occur in approximately equal numbers. In such localities the grey seal is probably more important than the harbour seal. The harp seal is about 100 to 200 times as numerous, while in the southwestern Gulf of St. Lawrence, as the combined populations of harbour and grey seals there. Despite this great numerical superiority the harp seal does not appear to be more important than the other seals as a host of *P. decipiens*.

The relation between each species of seal and the incidence of larval *P. decipiens* in Atlantic cod (*Gadus callarias*) is discussed.

INTRODUCTION

Atlantic cod, *Gadus callarias*, and other fishes along the Canadian east coast are commonly infected by larval ascarids, *Porrocaecum decipiens* (Scott, 1950). The larvae mature and reproduce in the stomachs of seals (Scott, 1953). A preliminary analysis (Scott, 1950) of the ascarids from the stomachs of a few seals showed that the parasite was widespread in the harbour seal, *Phoca vitulina*. It was present also in the only grey seal, *Halichoerus grypus*, examined. Subsequently, Fisher showed that harp seals, *Phoca groenlandica*, in the Gulf of St. Lawrence were also hosts for a species of *Porrocaecum* (FRB, 1951, pp. 29–31).

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J. Fish. Res. Bd. Canada, 15(4), pp. 495–516, 1958.
Printed in Canada.

These early studies established only the basic fact that the 3 common seals in this area were hosts of *Porrocaecum*. Since the seasonal and geographic distribution and the relative abundance of the 3 seals varied greatly, the relative importance of the species of seals as vectors of the parasite could not be determined at that time. Accordingly, to clarify this point, a larger collection of ascarids from seals' stomachs was begun in 1949 under the direction of the junior author and continued until 1956.

The present account summarizes our knowledge of the incidence of *P. decipiens* in the harbour, harp and grey seals in the Gulf of St. Lawrence, the Atlantic coast of Nova Scotia and the Bay of Fundy. We attempt also to assess the relative importance of each species of seal as vectors of *P. decipiens* in each of the foregoing areas.

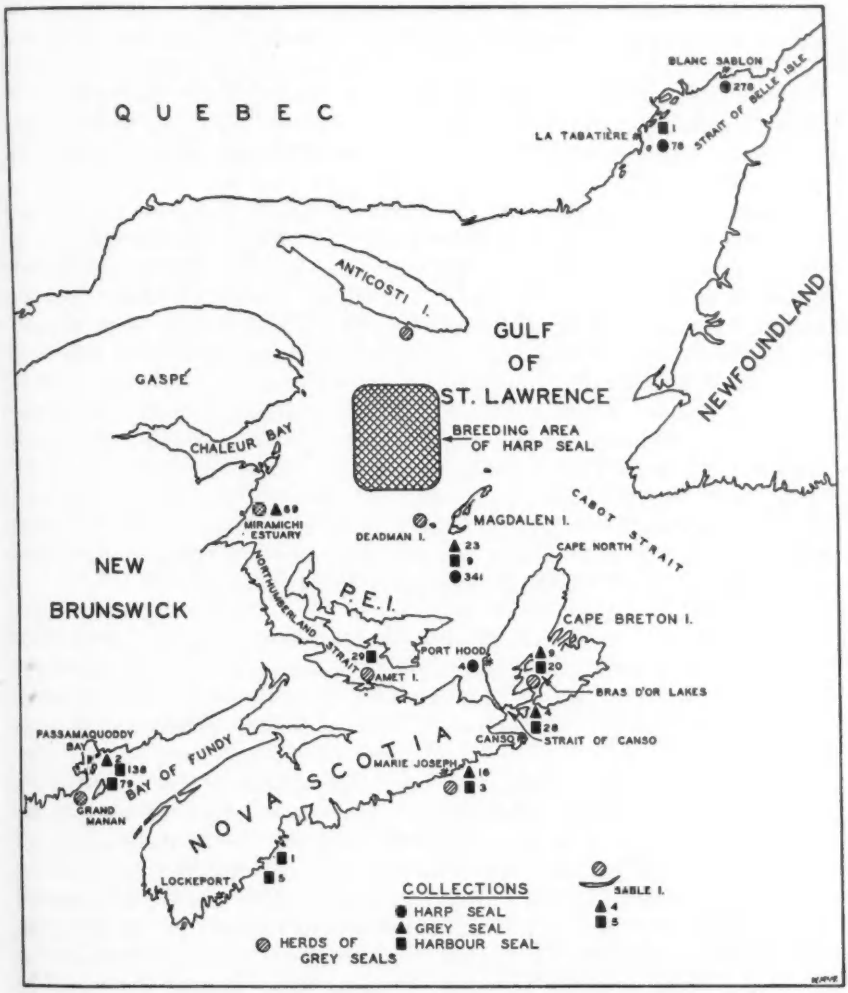
DISTRIBUTION AND ABUNDANCE OF SEALS

A summary of the distribution and abundance of the 3 most common seals along the Atlantic mainland of southern Canada is essential as a background for our interpretation of the results. When referring to different age-groups of seals, we shall use the following terms: *juvenile*–less than 3 months old; *immature*–older than 3 months but has never attained sexual maturity; *adult*–have reproduced at least once or would have mated for the first time in the breeding season of the year they were killed.

HARBOUR SEAL. This species is the most widely distributed of the 3 seals, being found more or less commonly throughout the year from the Bay of Fundy to the north shore of the Gulf of St. Lawrence. It seems to be most abundant in the lower Bay of Fundy around Grand Manan and the adjacent New Brunswick shore and along the Atlantic coast of Nova Scotia. In the Gulf of St. Lawrence the principal areas of concentration are in Northumberland Strait, in the Miramichi Estuary, around the Magdalen Islands, and around Anticosti Island. There is also a colony of unknown size at Sable Island. The total population in the Maritime Provinces in 1949 was estimated as consisting of 10,000 to 15,000 animals.

Harbour seals appear to be essentially non-migratory, although in some areas they carry out local migrations. For example, in early winter harbour seals enter the Bras d'Or Lakes, N.S., where they remain until early spring. No seals were observed there by the senior author during the portions of 4 summers spent in that area.

GREY SEAL. The grey seal is much more locally distributed (see accompanying Figure) than the harbour seal. There are no known breeding colonies in the Bay of Fundy apart from a small herd near Grand Manan. The grey seal is also rare along the Atlantic coast of Nova Scotia except on the northeastern part of the coast. Here, at Marie Joseph, several hundred immature and adult animals occupy the area from May until late fall. Along the northeast coast of Cape Breton Island, the species breeds commonly in January and February. As with the harbour seal, there is a colony of unknown size present in summer and winter at Sable Island. The principal areas of concentration are, however, in the south-



Distribution of seal collections, herds of grey seals and approximate breeding area of harp seals, along the southern Canadian mainland.

western Gulf of St. Lawrence. Here, 2 breeding groups are known: one usually around Amet Island in Northumberland Strait, and the other at Deadman Island near the Magdalen Islands. The former comprises about 2,000 adults and the latter probably at least 400 adults. In the summer a large herd of about 500 adults frequents the beaches extending north from the Miramichi Estuary. Grey seals in unknown numbers also occur around Anticosti Island. The total number of grey seals in the area considered in this paper is probably close to 7,000.

The grey seal is migratory. This is evident from the separation of breeding areas from regions of summer concentration. There is a pronounced fall movement of grey seals from the Gulf of St. Lawrence around Cape North and down along the northeast coast of Cape Breton Island. Some, possibly several hundred, enter the Bras d'Or Lakes in November. They remain there until about January. Then the seals move out of the lakes and presumably breed along the shores of Cape Breton Island.

HARP SEAL. This species, unlike the 2 preceding, performs long annual migrations. There are apparently 2 distinct groups of harp seals in the western Atlantic. One breeds on ice in the Gulf of St. Lawrence, the other on pack-ice off the northeast coast of Newfoundland. The former consists of about 1,000,000 immature and adult seals which enter the Gulf of St. Lawrence in January through the Strait of Belle Isle. Little is known about their subsequent behaviour until the adults reappear in early March to breed on the ice, usually north of the Magdalen Islands (Figure). During March the breeding adults apparently do not feed. Many seals drift on the ice towards Cape Breton Island and through Cabot Strait. Following the breeding season, harp seals of all ages move northwards. Some feed extensively on herring and flounders around the Magdalen Islands in April and May. They continue northwards and pass through the Strait of Belle Isle mainly in June. The harp seal thus spends no more than about 6 months annually in the vicinity of the Gulf of St. Lawrence.

EXTENT OF COLLECTIONS

This paper is based upon collections of ascarids from the stomachs of 318 harbour seals, 812 harp seals and 127 grey seals. The distribution and number of collections, excepting those from the east coast of Newfoundland, are shown in the Figure.

The collections were obtained in various ways. Most of the material from harbour and harp seals was purchased from seal hunters. A hunter removed the stomach, preserved it in formalin, attached the lower jaw to the stomach for identification of the seal and shipped the material to St. Andrews. Material was also collected in the field by H. D. Fisher and B. A. MacKenzie. We are indebted to Mr. Paul Montreuil of the Quebec Department of Fisheries for arranging the collection of stomachs from harp seals from the Magdalen Islands. Members of the Federal Department of Transport on Sable Island assisted us greatly by collecting stomachs from grey and harbour seals.

Collections of ascarids, especially those made in the field, were not always complete. Sometimes only a random sample was preserved. In other cases only some large identifiable worms were collected. In all cases, however, an estimate of the total number of worms in the stomach was recorded. The senior author found that the number of worms present in complete samples examined by him differed by about 10% from the estimate recorded when the collection was made.

Our studies are based entirely on the analysis of worms found in the stomachs of seals. No detailed examination and no collections were made of the ascarids which were occasionally observed in the duodenum. It was felt that these were

merely worms that had passed through along with food into the duodenum and that would subsequently be voided with the faeces. Furthermore, Scott (1953) adduced evidence that *P. decipiens* matures and lays eggs in the stomach of harbour seals. Hence, we believe that the incidence of *P. decipiens* in the stomach is a reasonable index of the importance of a particular seal as a host of *P. decipiens* and also of the recent contacts of that seal with *P. decipiens*.

IDENTIFICATION OF ASCARIDS

Several people shared in the identification of the ascarids in the collections. The junior author with Mrs. Jean Stuart made most of the identifications on material collected before 1953. The remainder of the early material and most of the collections made since 1953 were examined by the senior author. This material consisted of collections from 84 harbour, 39 grey and 274 harp seals. Miss B. J. Myers of the Institute of Parasitology, Macdonald College, Quebec, kindly identified material for us from 4 harbour and 16 grey seals in return for assistance in collecting material for use in her research on *P. decipiens*. Furthermore, Miss Myers has generously allowed us to use the results of her examinations of ascarids from the stomachs of 7 harbour, 199 harp and 23 grey seals from the Magdalen Islands. A brief account of her observations on ascarids in harp seals in 1956 has been published (Myers, 1957).

All the ascarids in each collection studied by us were not always examined. Only a few worms (about 10%) were selected for identification from many of the collections made between 1949 and 1952. These samples were frequently not randomly selected, but usually consisted of large identifiable stages. Since the samples were not always random, the results of these incomplete analyses have in most cases little quantitative value. Complete counts were made, however, of all worms in most collections examined by the senior author. With the exception of about 20 collections from which only large random samples were examined, the senior author has examined each worm in the collections available to him.

All generic identifications by the authors were made by examining worms with a binocular microscope of 13 magnifications. *Porrocaecum* and two other genera, tentatively identified as *Contracaecum* and *Anisakis* (rarely), were observed in the collections from all species of seal. A fourth, *Phocascaris*, may also have been present. This genus closely resembles *Contracaecum*. Since no critical examination was made of the diagnostic cephalic structures of ascarids other than *Porrocaecum*, some of the worms which we have designated as *Contracaecum* may have really been *Phocascaris*. Three stages were usually recorded for each genus: male, female and immature. Males were identified by their recurved tail, females by the presence of a vulva, and immatures by the absence of secondary sexual characters. *Porrocaecum* was distinguished from other ascarids by the presence of a short intestinal caecum and by the absence of an oesophageal appendix. These structures could be easily exposed by dissection of the anterior end of a worm. Additionally, the tail of female and immature *Porrocaecum* has a distinctive blunt end which readily distinguishes without dissection these stages of *Porrocaecum* from the other common genus, *Contracaecum*.

In the latter, the tail in females and in immature worms is sharply pointed. Female and immature *Anisakis* have a tail similar to that of *Porrocaecum*. However, judging from the number of male *Anisakis* observed, adult *Anisakis* are rare in seals. In the 1 or 2 collections in which several male *Anisakis* were observed, all worms with blunt posterior ends were dissected. It is therefore unlikely that many of the worms assigned by us to *Porrocaecum* were *Anisakis*.

In the collections examined by the senior author, with the exceptions noted earlier, all male ascarids were dissected. Females and immatures of different genera were distinguished mostly by the appearance of their tails. However, as a precautionary check, about 10% of the females and immatures were also dissected.

We have no assurance that uniform criteria for the differentiation of adult and immature ascarids were used by all who contributed identifications of ascarids for this paper. There was no appreciable difference in the ratio of adult to immature ascarids in a few collections which were separately examined by each of us. We feel reasonably confident, therefore, that the ratios of adults to immatures in collections examined by only one of us may be safely compared. On the other hand, the ascarids in most of the collections from the Magdalen Islands and Marie Joseph, N.S., were identified only by Miss B. J. Myers. We have not had an opportunity to examine her collections. Consequently, the ratio of adult to immature ascarids in her collections may be based on different criteria of maturity than those used by us. In comparisons between the collections examined by Miss Myers and those examined by us, the most useful values will be total values of all stages of *P. decipiens*.

No attempt was made to identify the species of ascarids present except for *Porrocaecum*. The senior author specifically identified, on the basis of the arrangement of post-anal papillae, 53 male *Porrocaecum* from 8 harbour seals from 4 areas, 52 male *Porrocaecum* from 9 grey seals from 4 areas and 7 male *Porrocaecum* from 6 harp seals from the Blanc Sablon area. All were *P. decipiens*. We believe, therefore, that most and probably all the *Porrocaecum* found in seals in the region considered belong to one species, *P. decipiens*. Accordingly, while recognizing the possibility that more than one species of *Porrocaecum* may be present in our collections, we shall refer all individuals of this genus to *P. decipiens*.

INCIDENCE OF *P. DECIPIENS* IN HARBOUR SEALS

P. decipiens was present in each of 221 collections of ascarids from harbour seals (Table I). Within these collections, *P. decipiens* made up 90 to 100% of the ascarids. The remainder were mainly immature stages of *Contracaecum* and *Anisakis*. Very few adult ascarids other than those of *P. decipiens* were observed.

The mean number of *P. decipiens* per stomach varied greatly. It ranged from 11 in 2 samples from Sable Island, N.S., to 634 in a single sample from southwestern Nova Scotia. High values were related to large numbers of immature *P. decipiens* rather than to overall high values for all stages. This was particularly evident in the samples from southwestern Nova Scotia, the Bras d'Or Lakes, and the Magdalen Islands. In samples from these areas, the ratio of immature to

TABLE I. Incidence and mean numbers of *Porrocaecum* in collection of ascarids from the stomachs of harbour seals (known juveniles excluded) from eight Canadian Atlantic areas. (Numbers of samples examined by Scott are in parentheses; unless otherwise noted, the remainder were examined by Fisher.)

Area	Complete or random samples								Incomplete, non-random samples				Percentage of all collections containing *Porrocaecum*
	Number of collections	Total number of ascarids	Number of ascarids identified	Frequency of *Porrocaecum* as a percentage of ascarids identified	Mean number per stomach of different stages of *Porrocaecum*[a] ♀	♂	Imm.	Total	Number of collections	Estimated total number of ascarids	Number of ascarids identified	Frequency of *Porrocaecum* as a percentage of ascarids identified	
	no.	*no.*	*no.*	%	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	%	%
Lower Bay of Fundy	76 (42)	3,729	3,729	97	11	13	23	47	58 (15)	6,316	1,405	99	100
Sable Island, N.S.	2 (2)	21	21	90	6	3	2	11	...	...	...	...	100
Southwestern Nova Scotia	1 (1)	634	634	100	0	11	623	634	6 (0)	400	59	97	100
Northeastern Nova Scotia	8 (2)[b]	424	424	98	12	9	31	52	20 (7)	1,003	378	93	100
Bras d'Or Lakes, N.S.	5 (4)	1,753	857	100	27	16	306	349	7 (0)	1,177	181	95	100
Northumberland Strait	5 (2)	82	82	100	3	3	10	16	24 (8)	1,401	287	97	100
Magdalen Islands, Que.	8 (0)[c]	822	822	93	4	4	88	96	...	...	...	...	87
La Tabatière, Que.	...	...	...	...	...	...	...	...	1 (1)	80	?	100	100

[a]Mean numbers for some collections have been calculated from the proportions of different stages present in random samples of the collections.

[b]Miss B. J. Myers examined 3 samples.

[c]Miss B. J. Myers examined 7 samples. One sample examined by H. D. Fisher has been omitted because in it the incidence of *Porrocaecum* was so high that its inclusion would have given a false impression of the average incidence of *Porrocaecum*. Approximately 95% of the 1,200 worms in this sample were *Porrocaecum*, of which about 60% were mature.

adult worms greatly exceeded that in any other samples. The numbers of adult worms were less variable. The mean number of adult *P. decipiens* in each stomach ranged from 6 in Northumberland Strait to 43 in the Bras d'Or Lakes. The mean for all areas was 17 adult *P. decipiens*.

The frequency distribution of the numbers of ascarids in harbour seals is shown in Table II. In this table, the estimated numbers of ascarids in stomachs from which no collections were made for identification have been added to the values upon which Table I is based. By so doing, the number of samples from different areas has been much increased. Since *P. decipiens* is almost the only ascarid present in harbour seals, the mean values for ascarids in Table II may be considered as approximating very closely to the values for *P. decipiens*.

TABLE II. Percentage frequency distribution and mean of the numbers of ascarids in the stomachs of harbour seals (known juveniles excluded) from nine Canadian Atlantic areas.

Area	Number of stomachs	Percentage of stomachs containing following numbers of ascarids						Mean no. of ascarids
		0–24	25–49	50–74	75–99	100–199	200+	
	no.	%	%	%	%	%	%	*no.*
Grand Manan, N.B.	79	38	29	13	...	14	6	77
Remainder of lower Bay of Fundy	125[a]	51	18	10	4	10	7	52
Sable Island, N.S.	5	80	20	...	...	...	...	20
Southwestern Nova Scotia	6	...	33	17	...	33	17	172
Northeastern Nova Scotia	31	35	16	23	10	13	3	52
Bras d'Or Lakes, N.S.	20	10	15	...	30	15	30	183
Northumberland Strait	29	38	21	17	10	4	10	49
Magdalen Islands, Que.	9	11	44	22	...	...	22	225
La Tabatière, Que.	1	...	...	...	100	...	...	80

[a]Eight stomachs had no ascarids.

Table II shows that the number of ascarids in stomachs from any area varied within wide limits. Considering only those areas represented by at least 10 samples, in all such areas, except the Bras d'Or Lakes, the majority of harbour seals had fewer than 50 worms. Usually, however, an appreciable number contained more than 100 or 200 worms. This was most noticeable in the samples from the Bras d'Or Lakes. Here, almost half the stomachs contained more than 100 worms. From this region the maximum number of worms, 1,261, almost all *P. decipiens*, was recorded.

The variation in the mean number of ascarids per stomach between areas with at least 10 samples, again excluding the Bras d'Or Lakes, was not great. It varied between 49 in Northumberland Strait and 77 in the vicinity of Grand Manan. Thus, there is little evidence of geographic variation in the incidence of *P. decipiens* in harbour seals.

There appears to be little seasonal change in the number of worms in harbour seals (Table III). An obvious seasonal trend can be seen only in the Grand Manan area. In this region numbers dropped from over 100 worms in the May to August period to less than 30 worms per stomach in September and October. In the adjacent area of the lower Bay of Fundy there was a less pronounced drop

in abundance at the end of the summer. Elsewhere there was no indication of regular seasonal changes in the numbers of ascarids.

TABLE III. Bi-monthly mean number of ascarids in the stomachs of harbour seals (known juveniles excluded) from six Canadian Atlantic areas. Numbers of stomachs examined are in parentheses

Area	Jan.–Feb.	Mar.–April	May–June	July–August	Sept.–Oct.	Nov.–Dec.
Grand Manan, N.B.	200(3)	...	137(15)	110(26)	24(23)	50 (1)
Remainder of lower Bay of Fundy	...	...	50(47)	61(49)	45(26)	25 (1)
Sable Island, N.S.	11(2)[a]	...	...	28 (2)	...	25 (1)
Northeastern Nova Scotia	...	33(3)	42(10)	29 (5)	78 (5)	65 (8)
Bras d'Or Lakes, N.S.	115(9)	103(7)	...	...	...	473 (4)
Northumberland Strait	...	...	39(12)	56(13)	53 (4)	...

[a]Collected in winter of 1956, exact month uncertain.

The number of worms per seal in the Bay of Fundy region was related to the sex of the host. This is clearly shown in Table IV. In the Grand Manan area, female harbour seals had 31 worms and males had 66. In the remainder of the lower Bay of Fundy, values were 46 for female and 65 for male harbour seals. In June, July, and August male seals were more heavily infected than female seals. In September and October, however, females had more worms than did the male seals.

Table IV also indicates that the breeding season does not apparently influence the number of ascarids in harbour seals. These seals breed in May and June. The values for ascarid infections in male and female seals in these months did not differ greatly from the mean values for all the summer months.

TABLE IV. Monthly mean number of ascarids in the stomachs of female and male harbour seals (known juveniles excluded) from adjacent areas of the lower Bay of Fundy. Numbers of stomachs examined are in parentheses.

	May	June	July	August	September	October	Mean
			Grand Manan				
Females	...	...	17 (6)	78 (4)	28(8)	17(6)	31
Males	...	...	61 (5)	218 (3)	10(5)	37(5)	66
			Remainder of lower Bay of Fundy				
Females	56(15)	35(18)	12(65)	22(13)	65(9)	35(2)	46
Males	...	61 (9)	47(13)	101(13)	56(7)	22(3)	65

Harbour seals become infected with ascarids within a few months of birth. A juvenile seal taken in July had 30 worms. Thirteen juvenile and immature harbour seals taken in the period from July to October had an average of 18 worms in their stomachs.

INCIDENCE OF *P. DECIPIENS* IN GREY SEALS

About 85% of the collections of ascarids from grey seals contained *P. decipiens* (Table V). This species made up between about 50 and 98% of the ascarids examined. The remainder were mainly adult and immature *Contracaecum*. In a few collections *Contracaecum* was the most abundant ascarid. Usually, however, in mixed infections *P. decipiens* was the most abundant species, being present frequently in very large numbers.

TABLE V. Incidence and mean numbers of *Porrocaecum* in collections of ascarids from the stomachs of grey seals (known juveniles excluded) from six Canadian Atlantic areas. (Numbers of samples examined by Scott are in parentheses; unless otherwise noted, the remainder were examined by Fisher.)

Area	Complete or random samples								Incomplete, non-random samples				Percentage of all collections containing *Porrocaecum*
	Number of collections	Total number of ascarids	Number of ascarids identified	Frequency of *Porrocaecum* as a percentage of ascarids identified	Mean number per stomach of different stages of *Porrocaecum*[a] ♀	♂	Imm.	Total	Number of collections	Estimated total number of ascarids	Number of identified ascarids	Frequency of *Porrocaecum* as a percentage of ascarids identified	
	no.	*no.*	*no.*	%	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	%	%
Lower Bay of Fundy	...	...	...	...	...	...	...	...	2 (1)	650	59	75	50
Sable Island, N.S.	3 (3)	253	253	98	19	29	35	83	...	...	...	...	100
Northeastern Nova Scotia	17 (2)[b]	3020	3020	89	33	27	99	159	2 (0)	708	52	18	100
Bras d'Or Lakes, N.S.	3 (1)	8816	7340	98	128	141	2627	2896	5 (0)	6410	195	72	100
Miramichi Estuary, N.B.	29 (29)	13782	7044	57	100	87	84	271	4 (3)	615	193	49	100
Magdalen Islands, Que.	23 (0)[c]	...	...	50±	7	3	...	...	...	...	...	...	50±

[a]Mean numbers for some collections have been calculated from the proportions of different stages present in random samples of the collections.
[b]Miss B. J. Myers examined 15 samples.
[c]Miss B. J. Myers examined all these samples.

The average number of *P. decipiens* varied between 83 in samples from Sable Island to 2,896 in the Bras d'Or Lakes. Intermediate values of 159 and 271 were recorded from samples from northeastern Nova Scotia and the Miramichi Estuary, respectively. The number of adult *P. decipiens* varied from 10 in the grey seals from the Magdalen Islands to 269 in those from the Bras d'Or Lakes. In the latter area the number of immature *P. decipiens* was about 10 times as great as the number of adults. Elsewhere, immature and adult *P. decipiens* were more equal in numbers.

The frequency of different numbers of ascarids in grey seals is shown in Table VI. It is obvious from this table that the number of ascarids may often reach very high levels in the grey seal. More than half the samples examined had more than 200 worms or more. Several, notably in the Bras d'Or Lakes, had more than 1,000 worms. The largest number of worms recorded, 5,244, was from the Bras d'Or Lakes. Almost all were *P. decipiens*.

TABLE VI. Percentage frequency distribution and mean of the numbers of ascarids in the stomachs of grey seals (known juveniles excluded) from six Canadian Atlantic areas.

Area	Number of stomachs	Percentage of stomachs containing following number of ascarids						Mean no. of ascarids
		0–49	50–99	100–199	200–499	500–999	1000+	
	no.	%	%	%	%	%	%	*no.*
Lower Bay of Fundy	2	...	...	50	...	50	...	325
Sable Island, N.S.	4	...	50	50	...	...	...	100
Northeastern Nova Scotia	20[a]	30	20	15	20	15	...	187
Bras d'Or Lakes, N.S.	9	...	...	...	...	33	67	1630
Miramichi Estuary, N.B.	69	3	10	16	41	17	13	496
Magdalen Islands, Que.	23[b]	30	17	26	17	9	...	158

[a]One stomach had no ascarids.
[b]Three stomachs had no ascarids.

There are insufficient data to permit analysis of the incidence of ascarids on a seasonal basis. Table VII suggests, nevertheless, that at all seasons of the year there are some grey seals which are heavily infected. Two adult male grey seals and 1 lactating female collected in January, 1954, during the breeding season at Amet Island, N.S., contained large numbers of ascarids. This indicates that the breeding season may not affect the incidence of ascarids in grey seals.

TABLE VII. Bi-monthly mean number of ascarids in the stomachs of grey seals (known juveniles excluded) from four Canadian Atlantic areas. Numbers of stomachs examined are in parentheses.

Area	Jan.–Feb.	Mar.–Apr.	May–Jun.	Jul.–Aug.	Sep.-Oct.	Nov.–Dec.
Northeastern Nova Scotia	...	...	210(17)	...	90 (2)	0(1)
Bras d'Or Lakes, N.S.	560(1)	...	...	...	...	2033(8)
Miramichi Estuary, N.B.	...	...	493 (4)	451(40)	528(20)	...
Amet Island, N.S.	700(3)	...	...	...	...	...

INCIDENCE OF *P. DECIPIENS* IN HARP SEALS

P. decipiens was almost completely absent from harp seals from the east coast of Newfoundland and Labrador (Table VIII). It was only observed in 2 of 111 stomachs of harp seals from this region.

TABLE VIII. Incidence and number of *Porrocaecum* in collections of ascarids from the stomachs of harp seals (known juveniles excluded) from the east coast of Newfoundland and Labrador. All samples were examined by H. D. Fisher.

Date	Number of collections	Estimated number of ascarids	Ascarids identified	*Porrocaecum* observed	Collections containing *Porrocaecum*
	no.	*no.*	*no.*	*no.*	%
Apr.–May, 1949	4	107	72	10	50
March, 1950	11	2,858	294	0	0
March, April, May, 1951	28	19,213	789	0	0
Mar.–Apr., 1953	68	...	...	0	0

Preliminary analysis of the ascarids from harp seals taken in the Gulf of St. Lawrence indicated that some of the variation in the incidence of *P. decipiens* was related to different periods of the reproductive cycle of the harp seal. Accordingly, we have grouped our data on the Gulf of St. Lawrence in terms of five periods of the reproductive cycle:

(i) *Prenuptial migration*–the southward movement of immature and adult harp seals which enter the Gulf of St. Lawrence in late December and early January.

(ii) *Prenuptial feeding*–the period between January and the whelping season in early March. It is not known if the main body of the seals is in the Gulf of St. Lawrence during this period. Some adults, however, are certainly present in the southwestern Gulf of St. Lawrence in early February.

(iii) *Nuptial*–from early March when the females begin to give birth to young on the ice until early April when the adult males have joined the females and copulation takes place. The whereabouts of the immatures in this period is unknown.

(iv) *Postnuptial feeding*–from early April to early May when many harp seals, both adult and immature, are in the vicinity of the Magdalen Islands.

(v) *Postnuptial migration*–the northward movement of adults and immatures at least some of which in June pass out of the Gulf of St. Lawrence through the Strait of Belle Isle.

The data for these five periods are summarized in Table IX. In Table IX and later in Table X the data for one adult female seal have been omitted. The stomach of this seal contained about 1,000 worms of which 62 were examined. All of these were *Porrocaecum*: 29 females, 12 males and 21 immatures. The inclusion of these data would have given a false impression of the mean number of *Porrocaecum*.

P. decipiens was not observed in the stomach of any southward-bound prenuptial migrant.

The numbers of immature and adult *P. decipiens* were high, averaging about 250 per stomach, in a sample of 4 stomachs of pregnant harp seals killed in the prenuptial feeding period.

The incidence of *P. decipiens* in the stomachs of adult harp seals in the nuptial season was always low. Their numbers averaged in different samples

TABLE IX. Incidence and mean numbers of *Porrocaecum* in collections of ascarids from the stomachs of harp seals (known juveniles excluded) from the Gulf of St. Lawrence at different stages of the reproductive cycle. Mean numbers for some collections have been calculated from the proportions of different stages present in random samples of the collections.

Date	Number of collections	Total number of ascarids	Number of ascarids identified	Percentage of stomachs containing *Porrocaecum*	Mean number per stomach of *Porrocaecum*				Mean number per stomach of other species					Examiner
					♀	♂	Imm.	Total	♀	♀	Imm.	Not classified	Total	
	no.	*no.*	*no.*	%	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	
Prenuptial migration;														
La Tabatière, Que.														
January, 1948	7	...	...	...	...	...	...	0	not recorded					Scott
January, 1950	21	581	168	...	...	...	...	0	...	...	...	28	28	Fisher
January, 1951	50	...	ca.500	...	...	...	...	0	not recorded					Fisher
Prenuptial feeding;														
Port Hood, N.S.														
February 17, 1950[a]	4	1,242	1,044	100	50	60	140	250	26	2	32	...	60	Fisher
Nuptial;														
Magdalen Islands														
March, 1949[c]	30	...	...	...	0	0	0	0	not recorded					Fisher
March 3–16, 1954[a]	6	2,759	2,759	33	0	0	1	1	54	52	354	...	460	Scott
March 12–23, 1956[a]	34	1,497	1,497	18	0	0	8	8	5	3	29	...	37	Myers
Mar. 14–Apr. 3, 1956[b]	21	454	454	10	0.3	0.1	1	2	3	3	14	...	20	Myers
Postnuptial feeding;														
Magdalen Islands														
April, 1951	6	1,200±	60	...	not recorded			165	not recorded				35	Fisher
April 21–May 16, 1952	74[c]	19,616	3,602	75+	1	1	22	24	...	...	...	242	242	Fisher
April 16–17, 1954	19	3,386	3,386	80+	31	14	...	...	not recorded					Wolfgang
April, 1955	9	960	396	...	5	4	10	19	23	8	57	...	88	Myers
Apr. 12–May 7, 1956	135	5,781	5,781	12	0.2	0.1	4	4	5	3	31	...	39	Myers
Postnuptial migration;														
Blanc Sablon, Que.														
June, 1948	4	...	...	...	...	...	...	0	not recorded					Scott
June, 1953	83	6,123	6,123	12	0.1	0.1	0.1	0.3	29	12	32	...	73	Scott
June, 1955	191	23,997	23,997	9	0.1	0.04	0.4	0.5	24	18	83	...	125	Scott

[a]All seals in these collections were adult females.
[b]All seals in this collection were adult males.
[c]One adult female has been omitted; see the text.

between 0 and 8 per stomach. Most were immature. Immature and mature stages of other ascarids were usually more numerous than *P. decipiens*.

There was considerable annual variation in the incidence of *P. decipiens* in stomachs of harp seals killed in the post-nuptial feeding periods around the Magdalen Islands. The percentage of stomachs containing *P. decipiens* varied from 12% in 1956 to more than 75% in 1952 and 1954. The lowest average number of *P. decipiens* per stomach was 4 in 1956. Values more than 10 times as great were recorded in 1951 and 1954. At this season, immature *P. decipiens* were always more numerous than adults. In 1952 and 1956, immature *P. decipiens* outnumbered adults by more than 10 to 1.

Our samples from the postnuptial feeding period unlike those from the nuptial period were drawn not only from adult seals, but also from immature and recently-born or juvenile seals. It was thought that non-breeding harp seals might play a different role than the adults with respect to *P. decipiens*. Accordingly, the data from the postnuptial feeding period have been analysed where possible in terms of three categories of seals: adult, immature, and juvenile. The individuals in these groups were distinguished on the basis of length and age using the minimum lengths and ages of harp seals at the attainment of sexual maturity as established by Fisher (unpublished studies). The samples were not taken continuously throughout the postnuptial feeding period but were taken, particularly in 1952, in several groups. We have therefore divided our data according to the time of collection to determine if there was any change in the incidence of *P. decipiens* with the advance of the postnuptial feeding period. A preliminary analysis of the data indicated that the incidence of *P. decipiens* was not related to the sex of the host. The males and females have therefore been grouped together in Table X.

TABLE X. The mean number of *Porrocaecum* in the stomachs of harp seals from the Magdalen Islands, related to the age of the seals and to the time of capture in the postnuptial periods of 1952 and 1956.

Date and capture and age group of seal	No. of collections	*Porrocaecum* per stomach ♀	♂	Imm.	Total	Other species, per stomach ♀	♂	Imm.	Total
1952	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*
April 21–30									
Adult	28[a]	1	2	30	33	...	...	...	256
Immature	14	0.3	0.1	4	4	...	...	...	128
Juvenile	4	0	0	2	2	...	...	...	28
May 5									
Age unknown	21	0	0	23	23	...	...	...	309
May 6–16									
Adult	5	1	0	34	35	...	...	...	185
Immature	6	1	0	13	14	...	...	...	248
Juvenile	1	1	7	9	17	...	...	...	3
1956									
April 12–25									
Adult	22	0	0	1	1	8	6	62	76
Immature	4	0	0	2	2	4	0	71	75
April 27–May 7									
Adult	83	0.1	0.04	0.5	0.6	4	3	27	34
Immature	20	0	0	0.4	0.4	5	3	16	24
Males, age unknown	5	4	3	80	87	2	1	5	8

[a]One adult female has been omitted; see the text.

Table X shows that *P. decipiens* was distinctly more common in 1952 in adult than in immature and juvenile seals. In 1956, there was little difference between adult and immature seals in the incidence of *P. decipiens*.

Some harp seals become infected with *P. decipiens* and other ascarids within a few weeks after birth. Of the 5 stomachs of juvenile seals available to us, 2 had no ascarids, 1 had 20 ascarids of which none were *P. decipiens*, 1 had 100 ascarids of which 9 were immature and adult *P. decipiens* and the fifth had 20 ascarids of which 17 were immature and adult *P. decipiens*.

There was no consistent difference between adult and immature harp seals with respect to the incidence of other species of ascarids in their stomachs. Generally, adult seals had more ascarids of other species, but in samples of May 6 to May 16, 1952, immature seals were more heavily infected than were the adult seals. The average number of ascarids in juvenile seals, as indicated earlier, was much lower than that in adult or immature seals.

There is no evidence that the incidence of *P. decipiens*, or of ascarids in general, usually increased with advance of time in the postnuptial feeding period. Furthermore, the incidence of reproductive stages of *P. decipiens* did not greatly change towards the end of the postnuptial feeding period. The only evidence of a substantial change in the incidence of *P. decipiens* is provided by the data for 5 juvenile seals in 1952 and for a group of 5 males of unknown age in 1956. In the juvenile seals, the incidence of *P. decipiens*, both adult and immature, was much higher in the single juvenile taken in May than in the specimens collected in April. This difference should, however, be regarded with caution since the sample was so small that it can hardly be considered as representative of the entire juvenile population. In May, 1956, 5 male harp seals of unknown age had very high incidences of *P. decipiens* as compared with incidences recorded earlier in April and at the same time in May from males and females of known maturity. This sample of males was collected from a different locality than were the other seals collected in the period April 27 to May 7. It thus cannot be regarded as representative of the harp seal population at that time.

P. decipiens was present in small numbers in about 10% of the collections of ascarids from northward-bound postnuptial migrants in 1953 and 1955.

Immature and mature ascarids of other species were much more numerous than *P. decipiens* in these samples.

To sum up, the incidence of *P. decipiens* in harp seals in the Gulf of St. Lawrence varied widely. Some of the variability, however, conformed to a seasonal pattern. In January and June during the migration of the harp seals through the Strait of Belle Isle, the incidence of *P. decipiens* in the stomachs of harp seals was very low. In the intervening months of February to May in the vicinity of the Magdalen Islands, *P. decipiens* was more frequently found, occasionally in large numbers, in the stomachs of harp seals.

RELATIVE IMPORTANCE OF EACH SPECIES OF SEAL

Porrocaecum decipiens occurred commonly at all seasons in almost all collections of ascarids from the stomachs of harbour and grey seals. Seals are the only known definitive hosts of *P. decipiens* on the Atlantic coast (Scott, 1956).

Therefore, where only harbour and grey seals occur they will be the only important hosts of adult *P. decipiens*. Since the harbour seal is the only common seal in the Bay of Fundy and along the southwestern coast of Nova Scotia, it must be the most important host of *P. decipiens* in those regions. Elsewhere the ranges of harbour and grey seals broadly coincide and the relative importance of each species is difficult to estimate. Grey seals are probably as common as harbour seals in northeastern Nova Scotia and in the southwestern Gulf of St. Lawrence. Moreover, the stomachs of grey seals contained on an average about 5 times as many adult *P. decipiens* as harbour seals. This suggests that in areas where both seals are present in approximately equal numbers, the grey seal is more important than the harbour seal as a vector of *P. decipiens*.

The problem of the relative importance of different seals as definitive hosts of *P. decipiens* is further complicated by the seasonal occurrence of large numbers of harp seals in the southwestern Gulf of St. Lawrence and possibly along the east coast of Cape Breton Island. They are probably about 100 to 200 times as abundant as the combined numbers in those areas of harbour and grey seals. The incidence of adult *P. decipiens* in the stomachs of harp seals in the southwestern Gulf of St. Lawrence was usually much lower than that in harbour and grey seals, both with respect to the percentage of harp seals so infected and to the numbers of adult *P. decipiens* in individual stomachs of harp seals. Nevertheless, in view of the large numbers of harp seals involved, the harp seal might be expected to be the most important host of *P. decipiens* in this region. However, the proportion of harp seals that carry adult *P. decipiens* is unknown. Furthermore, the length of time that harp seals act as hosts in the Gulf of St. Lawrence is not precisely known.

Although harp seals are presumably present in the Gulf of St. Lawrence from January to June, they apparently are not hosts of adult *P. decipiens* for this entire period. When harp seals enter the Gulf in January their stomachs are free of *P. decipiens*. Under experimental conditions *P. decipiens* required almost three weeks to mature in young harbour seals (Scott, 1953). Assuming that a similar period of time is required for *P. decipiens* to mature in harp seals and assuming also that harp seals ingest *P. decipiens* larvae soon after entering the Gulf, harp seals could become carriers for adult *P. decipiens* by the end of January. The only evidence that this happens was supplied by a sample from harp seals killed near Port Hood, N.S., in early February. These seals were heavily infected with adult *P. decipiens*, the larvae of which must have been ingested in the preceding month. In the breeding season in March, only a few immature and even fewer adult *P. decipiens* were found in the stomachs of adult male and female harp seals taken on the whelping ice in the Gulf. At first it was thought that this scarcity of *P. decipiens* was attributable to the fact that breeding seals do not feed very much (Fisher and Sergeant, 1954). This possibility is, however, precluded by the fact that adult, as well as immature, ascarids of other species were frequently present in large numbers in breeding harp seals. The facts thus indicate that the feeding of the adult harp seals prior to breeding had not generally brought them into frequent contact with *P. decipiens*. Apparently then, our February sample

was unusual in its high incidence of *P. decipiens* and should not necessarily be regarded as typical of the entire group of adult seals at that time.

It is only when breeding has been completed and a period of postnuptial feeding begins in April around the Magdalen Islands that *P. decipiens* appeared regularly in the stomachs of adult harp seals. At this time, immature seals were taken for the first time. In these *P. decipiens* was also present, in numbers approximately the same as those in the adult seals, both with respect to total numbers of *P. decipiens* and to the ratio of adult *P. decipiens* to immature *P. decipiens*. Although we have no empirical evidence of the whereabouts of the immature seals during the breeding season it would appear that they, like the adult seals, had not previously been in extensive contact with *P. decipiens*. Accordingly immature seals do not seem to be more important than adult seals as hosts of *P. decipiens* in the period from January to April.

It is noteworthy that immature *P. decipiens* greatly outnumbered adults in most of our collections from adult and immature seals in the postnuptial feeding period. The ratio of adult to immature *P. decipiens* was markedly lower than that observed in harbour and grey seals where adult and immature stages of *P. decipiens* were usually nearer to each other in numbers. It suggests that the *P. decipiens* in harp seals at this time had been so recently-ingested that they had not had time to become mature. It is noteworthy also that there was no increase in the numbers of *P. decipiens*, either adult or immature, as the postnuptial feeding period advanced. This indicates that the harp seals in these samples were transients and that the samples were drawn from successive waves of migrants. Thus, it would appear that the entire population of harp seals is not continuously present around the Magdalen Islands in the postnuptial feeding period.

The incidence of *P. decipiens* was always low in harp seals taken when leaving the Gulf of St. Lawrence through the Strait of Belle Isle in the latter part of June. This low incidence contrasts strikingly with the higher incidences recorded several weeks earlier near the Magdalen Islands. The reasons for this difference are unknown.

Whatever the reasons may be, it is obvious that the harp seal, by virtue of its northward movement from the Magdalen Islands in May, becomes decreasingly important in the late spring as a host of *P. decipiens* in the southwestern Gulf of St. Lawrence.

The facts indicate that the harp seal is an important host of *P. decipiens* mainly during the postnuptial feeding period around the Magdalen Islands. Unfortunately, however, we do not know if the seals caught at this time are representative of the entire Gulf population of harp seals. There is some evidence that they are not. First, our samples from the postnuptial feeding period in this area show that adult seals outnumbered immature by about 3 to 1 (Table X). But Fisher and Sergeant (MS, 1954) have indicated that adult and immature harp seals are present in about equal numbers in the Gulf population when it enters the Gulf in early winter. Thus, it appears that a substantial part of the population of immature seals does not migrate northward close to the Magdalen

Islands. Secondly, the remarkable difference in the incidence of *P. decipiens* between the harp seals from the Magdalen Islands and those from the Strait of Belle Isle suggests that the former are an unrepresentative, heavily-infected group.

A rough estimate of the relative importance of each of the three seals as a vector of *P. decipiens* in the southwestern Gulf of St. Lawrence can be made. Harp seals are commonly infected with *P. decipiens* only during the postnuptial feeding period, that is for about two months. This period during which eggs of *P. decipiens* can be distributed by harp seals is about only one-sixth as long as that of harbour and grey seals. The average numbers of adult female *P. decipiens* in the stomachs of harbour and grey seals were respectively 11 and 55. It is difficult with our present knowledge to make a reliable estimate of the average number of adult female *P. decipiens* in harp seals. This is so because of the small size of our samples relative to the total population of harp seals and also because of the apparent large annual variation in incidence. The samples from the postnuptial feeding periods of 1952 and 1956 are probably the most representative from the point of view of the number of specimens and the portion of the postnuptial feeding period that was covered by the samples. In these years, the average number of adult female *P. decipiens* was 1 and 0.2, respectively, for 1952 and 1956. The populations of the three seals in the southwestern Gulf of St. Lawrence are approximately 3,000 harbour seals, 6,000 grey seals and 1,000,000 harp seals. Using these values we estimate that, at any one time during the period when all three species of seal are hosts of adult *P. decipiens*, there are about 30,000 adult female *P. decipiens* in harbour seals, about 300,000 in grey seals, and between 200,000 and 1,000,000 in harp seals. Since harbour and grey seals are hosts throughout the entire year and whereas the harp seal appears to be an important host for only 2 months each year, the value for the harp seal should be divided by 6. This gives a value between about 35,000 and 175,000.

The populations of female *P. decipiens* in the stomachs of each seal are assumed to be indicative of the importance of each species of seal as a host of *P. decipiens*. We assume also that *P. decipiens* reproduces throughout the entire year. From our calculations, it appears that in the southwestern Gulf of St. Lawrence the grey seal is the most important and the harbour seal the least important host of *P. decipiens*. The foregoing estimates are undoubtedly subject to wide error. They seem, however, realistic enough to indicate that the importance of the harp seal is certainly not nearly as great as might be expected solely on the basis of its great numerical superiority over the other seals. A more accurate estimate of the importance of harp seals cannot be made until further collections of harp seals during the postnuptial feeding period have been made.

RELATION OF SEALS TO INFECTED COD

The importance of each species of seal in relation to the incidence of larval *P. decipiens* in cod from different fishing grounds off the Canadian Atlantic mainland cannot be clearly estimated. However, in some areas, certain species

of seals seem to be responsible. To appreciate this relationship there follows a summary of the incidence of larval *P. decipiens* in Atlantic cod, based on Scott and Martin (1957). The percentage of market cod fillets infected with larval *P. decipiens* is about 7% on the offshore Nova Scotian Banks, 15% around Lockeport in southwestern Nova Scotia, 25% in northeastern Nova Scotia and about 45% at present in the southwestern Gulf of St. Lawrence. The greatest infection occurs in the Bras d'Or Lakes where almost 100% of cod are infected. Moreover, the average number of nematodes per fillet in Bras d'Or Lake cod is at least 5 times greater than in cod from the Gulf of St. Lawrence (Scott and Black, unpublished data).

The incidence of infected cod in offshore waters is low, presumably because of the offshore scarcity of seals. The species of seals responsible for this light infection are unknown because we do not know where the cod from these banks acquire their infection. Harbour and grey seals resident on Sable Island may contribute in offshore areas to the infection. Many offshore cod are migratory (McKenzie, 1956) and some may become infected during migrations either to inshore waters along the Nova Scotian coast or to the Gulf of St. Lawrence.

The harbour seal is the only common seal in the Bay of Fundy and along the shores of southwestern Nova Scotia. Since the inshore cod of these regions are essentially non-migratory (McCracken, 1956; McKenzie, 1956) they must become infected in these regions. Therefore, the harbour seal must be responsible for most, if not all, of the *P. decipiens* larvae in cod in these regions. In these regions, relatively small numbers of harbour seals account for high incidences of infection in cod. In the lower Bay of Fundy, the total population of harbour seals probably numbers less than 1,000. Here, about 65% of market cod fillets are infected with larval *P. decipiens*. Along southwestern Nova Scotia there are probably about 2,000 harbour seals. Although the overall incidence of infected fillets in this region is about 15%, in the inshore waters of this region about 35% of market cod fillets are infected with *P. decipiens* (Scott and Martin, 1957).

For northeastern Nova Scotia, a definite relationship between the incidence of infection in cod and the presence of a particular species of seal cannot be shown. Many cod along the east shore of Cape Breton Island are migratory, some moving in and out of the Gulf of St. Lawrence, others migrating to the off-shore banks (McKenzie, 1956). Harbour, grey, and possibly harp seals are present along the east coast of Cape Breton. Only in the Canso area, where most cod are localized in their distribution (McKenzie, 1956) can a relationship between specific seals and infected cod be suggested. Around Canso the incidence of larval *P. decipiens* in cod is about 25%. Both harbour and grey seals live in this area and are apparently responsible for an incidence in cod which is higher than that for southwestern Nova Scotia where only the harbour seal is found. This suspected relationship may not be real since harp seals occasionally drifted on ice during late March and April through the Strait of Canso before the Canso causeway was built. Thus, harp seals may have been responsible for some of the infection in cod around Canso.

A clear relationship exists between infected cod and harbour and grey seals in the Bras d'Or Lakes. In this region there are several local populations of cod apparently confined to the Lakes (Scott and Black, unpublished data). By far the highest infection in cod has been noted here. A few hundred harbour and grey seals spend 2 or 3 winter months in the Lakes. Collections of ascarids from these seals contained the greatest numbers of *P. decipiens* recorded from any region. As grey seals in the Bras d'Or Lakes are known to feed on cod (Fisher, unpublished data), there is an evident relationship between the exceptionally high incidences in grey seals and cod from that area. Thus relatively few seals, when concentrated—even if for only a short time, are capable of producing exceedingly heavy infections in cod.

In the Gulf of St. Lawrence, the harp seal at first sight appears responsible for the high incidence of larval *P. decipiens* in cod. However, it is surprising, in view of the incidence of infection that can be produced in cod elsewhere by the relatively scarce harbour and grey seals, that a million harp seals should not produce a much higher incidence in cod in the Gulf of St. Lawrence. Indeed, if harp seals were entirely absent from the Gulf of St. Lawrence, the higher incidence in cod there than elsewhere would be quite consistent with the fact that the centre of abundance of grey seals is in the southwestern Gulf of St. Lawrence. It is suggestive that cod caught on several occasions between 1945 and 1957 in inshore waters northeast of the Miramichi Estuary, where we found several hundred harbour and grey seals concentrated in the summer, were much more heavily infected than cod from further offshore (Scott and Martin, 1957). In conclusion, we feel that it would be unwise to assume that because the harp seal is much more common than the other seals that its importance in relation to infected cod is necessarily proportionately greater. Further studies of the incidence of *P. decipiens* in harp seals, of the distribution of the harp seal within the Gulf of St. Lawrence, and of the relation of the distribution of seals to infected fish in this area are required.

SUMMARY

The distribution and abundance of harbour, harp and grey seals in the Bay of Fundy, along the coast of Nova Scotia, and in the Gulf of St. Lawrence are briefly described. Estimates of the numbers of each species are 10,000 to 15,000 harbour, 1,000,000 harp and 7,000 grey seals.

Ascarids in collections from the stomachs of 318 harbour, 812 harp, and 127 grey seals from the aforementioned regions were identified. *Porrocaecum* and two other genera of ascarids, tentatively identified as *Anisakis* and *Contracaecum*, were found in the three species of seals. All of 112 male *Porrocaecum* that were identified to species were *P. decipiens*. This species was identified in each species of seal.

Harbour seals were almost always infected with *P. decipiens*. The number of *P. decipiens* in each stomach varied greatly but usually there were about 50 in a seal. About half of the *P. decipiens* were mature. There was no evident geo-

graphic variation in the numbers of *P. decipiens* per stomach. No widespread seasonal changes in the incidence of *P. decipiens* were noted. Male harbour seals had more *P. decipiens* than female seals. Young harbour seals were hosts of *P. decipiens* in their first summer.

Grey seals, like harbour seals, were usually infected with *P. decipiens*. The numbers of *P. decipiens* per stomach varied from an average of 83 in grey seals from Sable Island to 2,896 in those from the Bras d'Or Lakes. Grey seals from the Miramichi Estuary had 271 *P. decipiens* per stomach, almost twice as many as in grey seals from northeastern Nova Scotia. Between 40 and 70% of the *P. decipiens* were adult except in the samples from the Bras d'Or Lakes where about 10% were adult. Large numbers of ascarids were present in grey seals at all seasons.

In harp seals from the Gulf of St. Lawrence the incidence of *P. decipiens* showed much variation, most of which was seasonal in nature. Accordingly, we summarize these results in terms of five phases of the reproductive cycle of the harp seal, as follows:

PRENUPTIAL MIGRATION: *P. decipiens* was not observed in 78 harp seals collected in January as they migrated southwards through the Strait of Belle Isle.

PRENUPTIAL FEEDING: *P. decipiens* was present in large numbers in each of 4 harp seals killed in early February.

NUPTIAL PERIOD: *P. decipiens* was present in about 10% of the 91 stomachs of breeding harp seals killed in March and early April. The average number of *P. decipiens* per stomach did not exceed 8 in any sample and was usually much lower. Adult *P. decipiens* were found in only 1 stomach. The incidence of *P. decipiens* was similar in breeding male and breeding female seals.

POSTNUPTIAL FEEDING PERIOD: *P. decipiens* was observed most frequently in harp seals feeding around the Magdalen Islands in April and May. In 1952 and 1954 more than 75% of the 93 harp seals examined contained *P. decipiens*, but in 1956 *P. decipiens* was found in only 12% of the 135 stomachs examined. In 1952 an average of 2 adult *P. decipiens* per stomach was recorded; in 1954, 45 adult *P. decipiens* were present; and in 1956, 0.3 adult *P. decipiens* were recorded. Immature *P. decipiens* usually outnumbered adults by about 10 to 1. No large differences between the incidence of *P. decipiens* in adult and that in immature seals were observed.

POSTNUPTIAL MIGRATION: *P. decipiens* was found in about 10% of 278 stomachs of harp seals collected in 1953 and 1955 during their northward migration through the Strait of Belle Isle. The average number of *P. decipiens* per stomach was about 0.4 of which about two-thirds were immature.

P. decipiens was observed in less than 2% of 111 stomachs of immature and adult harp seals collected from the east coast of Newfoundland.

The relative importance of each seal as a vector of *P. decipiens* is considered. The harbour seal is unquestionably the most important in the Bay of Fundy and along the coast of southwestern Nova Scotia. Where harbour and grey seals occur together in approximately equal numbers, the grey seal by virtue of its heavier infections is probably more important than the harbour seal. The harp seal, although it is much more numerous than the other seals, does not appear

to be more important than grey and harbour seals as a host of *P. decipiens* in the southwestern Gulf of St. Lawrence.

The relation between seals and the incidence of larval *P. decipiens* in cod is discussed. Harbour seals in the Bay of Fundy maintain incidences of about 65% in cod in some areas. Along southwestern Nova Scotia, the presence of harbour seals alone is associated with incidences of 15% in cod or even higher in some inshore localities. A few hundred harbour and grey seals, seasonally concentrated in the Bras d'Or Lakes, appear to be responsible for an incidence of *P. decipiens* of almost 100% in cod from that region. The high incidence (about 45%) of *P. decipiens* in cod in the southwestern Gulf of St. Lawrence is associated with the seasonal occurrence in this region of about a million harp seals and also with the concentration of grey seals in that area.

ACKNOWLEDGMENTS

We are indebted to Mr. Paul L. G. Montreuil, Director, Marine Biological Laboratory, Quebec Department of Fisheries, Grindstone, Que., for his efforts and co-operation in obtaining seal stomachs from the Magdalen Islands. Mr. Antoine Jones, Quebec Department of Fisheries, Blanc Sablon, Que., made possible the collection of stomachs from the northward migration of harp seals through the Strait of Belle Isle. Miss B. J. Myers, Institute of Parasitology, Macdonald College, Que., kindly made available to us data from various seal collections from the Magdalen Islands in 1956. We are grateful for the assistance of the Federal Department of Transport, through its members at Halifax and on Sable Island, in collecting stomachs from grey and harbour seals at Sable Island. Mrs. Jean Stuart carried out most of the identifications on material collected before 1953. Mr. B. A. Mackenzie undertook much of the field work involved in the collections from all three species of seals under study here, and assisted in much of the preliminary treatment of the material.

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Round Haddock Landings in Newfoundland: Quantity and Quality Relative to Gutted Haddock[1]

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ABSTRACT

Late in 1953 when large haddock became scarce on the Newfoundland banks, fish plants, which previously had found haddock less than 45 cm. (18 in.) in length to be unacceptable for filleting, began to handle quantities of smaller haddock, 33 to 43 cm. (13 to 17 in.), and generally in an ungutted condition.

Determination of the trimethylamine values of fillets from round and gutted haddock showed average values of 0.66 mg. per 100 g. of fillets for round and 0.73 for gutted fish from research vessel and 1.39 for round and 1.61 for gutted from commercial trawlers. These differences were not statistically significant. Using trimethylamine values as indicators of spoilage, round haddock were kept under ice up to 9 days under experimental conditions and produced unspoiled fillets.

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HADDOCK LANDINGS

Introduction

Prior to the autumn of 1953, in Newfoundland fresh fish plants the commercial requirements for haddock, *Melanogrammus aeglefinus* (L.), were such that only fish 45 cm. (18 in.) and larger (fork length) were acceptable for filleting. All haddock were gutted before landing. This has been the custom for trawler-caught haddock both in Newfoundland and in the Maritimes. Late in 1953, however, large haddock became extremely scarce on the Newfoundland banks. The scarcity of large fish occurred at a time when haddock of the numerous 1949 year-class were abundant on the Grand Bank and extremely abundant on St. Pierre Bank.

Haddock of the 1949 year-class were small, mainly between 33 and 43 cm. (13 and 17 in.) in 1954, and the small quantities which could be gutted at sea made fishing for them unprofitable. For many years the Biological Station at St.

[1]Received for publication November 18, 1957.

J. Fish. Res. Bd. Canada, 15(4), pp. 517–527, 1958.
Printed in Canada.

John's had been bringing in round haddock, carefully iced, on the research vessel *Investigator II* for examination at the Station, and fillets removed from these fish at the Station had been found to be in excellent condition. Upon the advice of the Biological Station, a local fish plant in the latter part of 1953 began landing haddock in the round condition and other plants soon followed. Filleting plants which previously found haddock less than 45 cm. (18 in.) unacceptable now began to handle quantities of the smaller haddock, about 33 to 43 cm. (13 to 17 in.) in length, and generally in the ungutted condition. The adoption by some plants of machine filleting of these young haddock made them more acceptable to these plants.

The acceptance of small, round haddock has persisted to the present time and spread gradually to the Nova Scotian area. Because of the abundance of small and the scarcity of large haddock in the catch from the Newfoundland banks it gradually became the custom to land both small and large haddock in the ungutted condition.

Landings, January 1953 to December 1956

The main fishing grounds for haddock in the Newfoundland region are situated on the southern half of the Grand Bank (ICNAF Subdivisions 3O and 3N), and on the deep water, southwestern slope and the shallow water plateaus of St. Pierre Bank (ICNAF Subdivision 3P). Although Spanish otter trawlers catch considerable quantities of haddock in Subdivision 3N, most of the Newfoundland haddock catch comes from the southwestern part of 3O and from 3P.

Landings of haddock by Newfoundland trawlers in 1953 were quite low because of the scarcity of fish large enough to meet the commercial size requirements of the time. Late in 1953 the landing of small, round haddock was begun. At first, fish plants were somewhat hesitant to handle large quantities of the small fish, and the amounts brought in were restricted. Thus, in the last three months of 1953, only about 30% of the weight of haddock landed was made up of small, round fish. However, as difficulties in handling and processing were overcome, and with the advent of the "fish stick", landings of the small and usually round fish increased. Table I and the accompanying Figure show landings of round and gutted haddock, 1953 to 1956.

From January to September, 1954, varying amounts ranging from 50 to 80% of the total weight of haddock landed consisted of the small, round fish. During the first half of the year over half the haddock landed were from the Grand Bank. Because of the distance of the grounds from the port and consequent long trips, captains were instructed to restrict the keeping of small, round haddock to the latter part of each trip. From June to December, 1954, the main fishery for haddock was concentrated on St. Pierre Bank, much closer to the fresh-fish plants on Newfoundland's south coast and within range of the smaller otter trawlers which could not readily undertake the longer trips to the Grand Bank. Shorter trips were now possible and great effort was concentrated on the catching of haddock, catches of 10,000 lb. and over in an hour's dragging being common. With the arrival of the colder autumn and winter months the small fish could be

TABLE I. Haddock landings in Newfoundland, 1953 to 1956, from the Grand Bank (ICNAF Subdivisions 3L, 3N, 3O), St. Pierre Bank (ICNAF Subdivision 3P), Nova Scotian banks and Gulf of St. Lawrence (ICNAF Subarea 4). One million pounds = 453,592 kg. = 453.592 metric tons.

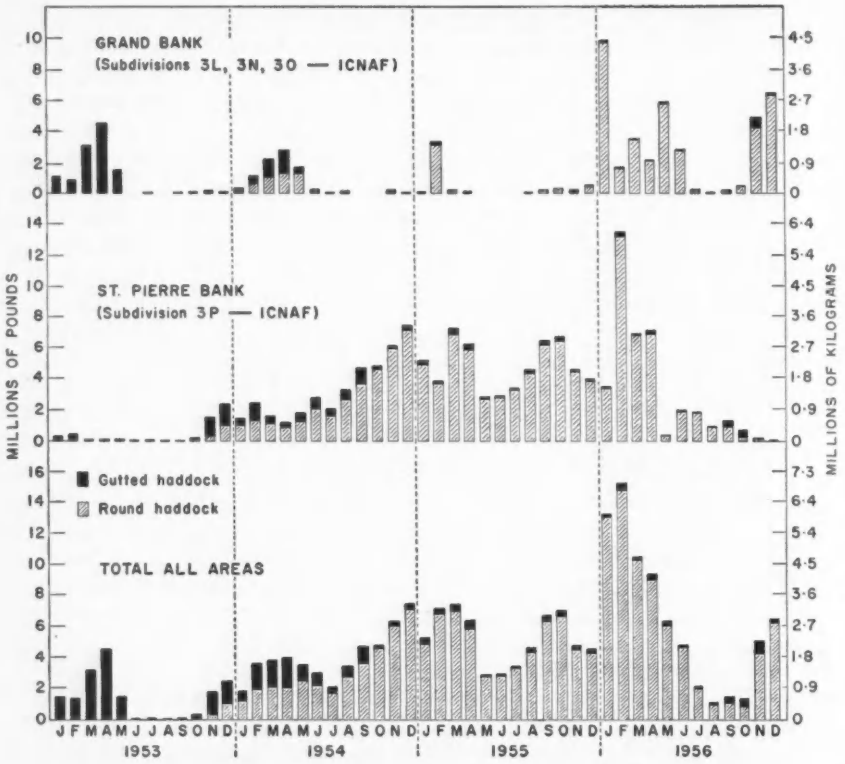
Months	Total haddock, all areas	Proportion of total caught			Proportion landed round			
		Grand Bank	St. Pierre Bank	N.S. banks and Gulf	Grand Bank	St. Pierre Bank	N.S. banks and Gulf	Total, all areas
	pounds	%	%	%	%	%	%	%
1953								
Jan.–Mar.	6,078,386	85	15	...	0.1	0	...	0.1
Apr.–June	6,063,078	98	1	0.2	0	0	0	0
July–Sept.	55,311	37	63	0.1	0	0	0	0
Oct.–Dec.	4,588,160	7	91	2	12	33	0	31
1954								
Jan.–March	9,182,687	40	60	...	53	64	...	60
April–June	10,426,076	44	55	0.05	58	75	0	67
July–Sept.	10,251,770	1	99	0.02	100	79	0	79
Oct.–Dec.	18,762,702	1	99	0.01	83	96	0	96
1955								
Jan.–Mar.	19,846,105	18	82	...	95	95	...	95
April–June	12,080,874	1	99	0.5	40	96	0	95
July–Sept.	14,670,160	1	99	0.02	87	96	43	96
Oct.–Dec.	16,308,137	6	94	0.001	94	97	0	97
1956								
Jan.–Mar.	38,944,615	38	62	...	99	98	...	99
April–June	20,471,739	52	46	2	99	97	28	97
July–Sept.	4,464,292	8	91	1	98	90	97	91
Oct.–Dec.	12,744,688	92	7	0.4	94	40	63	90

kept longer before being processed. The combination of these factors resulted in the abandonment of the restrictions on landing and much larger quantities of round haddock were landed. Thus, in October 1954 the landings of small, round fish amounted to 96% of the total weight landed and continued at this high level for the remainder of the year.

The excellent fishery for haddock which had begun on St. Pierre Bank in 1954 was continued there throughout 1955. With short trips and large catches still being made, the proportion of each monthly catch landed round continued to be high, usually above 95%. In fact, the quantities of haddock which were brought in gutted in most months were reduced to as low as 1 or 2% of the total weight landed.

The majority of the fish landed were of the extremely abundant 1949 year-class. The modal length of the fish landed in 1954 was about 39 cm. (15½ in.); in 1955, about 42 cm. (16½ in.); and in 1956, about 43 cm. (17 in.). In 1955 the increase in size brought the larger fish of the 1949 year-class to the previous commercial minimum size of 45 cm. (18 in.) for gutted fish. However, the price difference (2½ to 3 cents per pound for gutted fish, 1¾ cents for round fish) did not induce fishermen to undertake the extra effort on board ship of gutting other than small numbers of these haddock as long as the large catches continued.

Haddock were abundant on St. Pierre Bank and Grand Bank in the early months of 1956. Otter trawlers continued to land large quantities, 98 to 99% by weight being round. Following this the haddock fishery became poor, with


GRAND BANK
(Subdivisions 3L, 3N, 3O — ICNAF)
ST. PIERRE BANK
(Subdivision 3P — ICNAF)
Gutted haddock
Round haddock
TOTAL ALL AREAS
MILLIONS OF POUNDS
MILLIONS OF KILOGRAMS
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1953
1954
1955
1956

Otter-trawler landings in Newfoundland of round and gutted haddock, 1953 to 1956. Gutted haddock expressed in round weight for comparison. (1 million pounds = 453,592 kg. = 453.592 metric tons.)

smaller quantities being caught. This resulted in a somewhat larger than usual proportion of the catch being gutted, but by December, when good haddock fishing was experienced on Grand Bank and large catches were being procured again, the round fish amounted to 99% of the total landed.

Before World War II the haddock landings in Newfoundland were small incidental catches obtained in the fishery for cod, and most of the haddock was processed by salting. Landings of haddock for fresh filleting were begun after the war with the introduction of the otter trawler. Landings increased from just over a million pounds in 1945 to a high of 28 million pounds in 1949. These landings were made up mainly of large haddock from a virgin stock. By 1951, however, the effects of the fairly intense fishery were beginning to show and were reflected in the small landings for the year of just over 7 million pounds, the lowest for a number of years. In 1952 and 1953 larger quantities of somewhat smaller haddock, of a size previously discarded, were brought in. As a result the

landings were increased to about 16 million pounds in 1953. By the end of 1953, however, even these haddock were so scarce that, had the commercial size restrictions remained the same, landings would have dropped to the lowest level in recent years. Landing of small haddock, mainly round, resulted in a considerable increase in the yearly total of haddock landings to about 50 million pounds in 1954, 63 million pounds in 1955, and 77 million pounds in 1956.

QUALITY OF FILLETS

Introduction

The landing of round haddock raised questions regarding the relative quality of fillets from round fish and from the previously usual gutted haddock. Consequently a number of tests of the trimethylamine (TMA) values of the fillets from round and gutted haddock were made. These tests were carried out both on haddock caught by the research vessel *Investigator II* and kept carefully iced, and on fillets of commercial haddock landed by commercial trawlers at St. John's.

The TMA estimations were done by the Federal Department of Fisheries Fish Inspection Laboratory at St. John's under the direction of Mr. John P. Hennessey.

TMA was determined by the colorimetric method (Dyer, 1945).

Beatty and Gibbons (1937) showed that the amount of TMA forms a useful index for the measurement of spoilage in the body muscle of the cod, *Gadus callarias* L.

Castell and Triggs (1955) found that in fillets of haddock, *Melanogrammus aeglefinus* (L.), TMA was a more sensitive measure of early spoilage than either organoleptic examination or pH. They review the relevant literature and conclude that haddock fillets with 0 to 0.9 mg. TMA nitrogen per 100 g. of fillet (TMA value) are in a fresh condition; those with TMA values between 1.0 and 4.9 are edible but spoiling, while those with TMA values above 5 are spoiled.

Samples from the *Investigator II*

Haddock were caught with otter trawl in half-hour sets on the Grand Bank and St. Pierre Bank in May and June by the *Investigator II*. As soon as possible after capture some of these haddock were gutted and washed. These gutted haddock, and the same number of washed, round haddock of similar size to the gutted and from the same set, were placed immediately in the hold of the vessel and iced carefully in aluminum fish boxes. The groups of round and of gutted haddock from a single set were placed in separate boxes and were re-iced when necessary. Upon landing, the fish were removed from the ice and filleted immediately. The skin was removed and the fillets were trimmed in the usual way. TMA examination was either carried out immediately or the fillets were preserved in a deep-freeze at –18°C. pending TMA determination, which was carried out individually on minced samples of both fillets (combined) from each fish.

All the average TMA values for the round haddock, even up to 7, 8 and 9 days under ice, were below 1, while for the gutted haddock the TMA values for 8 and 9 days were 1.57 and 1.37 respectively. After 8 days storage in ice TMA values for fillets of individual round haddock reached as high as 1.05 while the lowest individual value in a sample of five was 0.44; for gutted haddock the corresponding values were 2.22 and 0.73. After 9 days storage highest and lowest TMA values in samples of five haddock were 0.82 and 0.50 for round and 2.86 and 0.55 for gutted (Table II).

In the individual sample comparisons given in Table II the only significant differences between the averages of the TMA values of round and gutted haddock are in Sample A after 6 days (at the 1% level), and in Sample C after 8 days and 6 days (at the 5% and 1% levels respectively). In two of these samples the value for round exceeds that for gutted and for one the value for gutted exceeds that for round. In the totals in Table II, for the same periods of storage, only the differences in the averages of TMA values for 5 to 7 days and for 8 to 9 days are significant (both at the 1% level). In the former the TMA value for round is greater and in the latter the value for gutted is the greater.

In the overall comparisons of all the data in which there were equal numbers of round and of gutted haddock in each sample (Table IV), the average TMA value for round haddock, 0.66, is lower, but not significantly lower, than the value for gutted haddock, 0.73.

Inspection of the range of TMA values for round and gutted haddock in the various samples described in Table II indicates that in spite of the careful icing some of the differences may be due to differences in icing.

It is evident that, for the usual type of bacterial spoilage as indicated by TMA values, with very careful icing round haddock may be kept under ice as long as 9 days and still yield fillets in the fresh, unspoiled condition. There is no evidence that fillets from round haddock after storage in ice for 8 or 9 days have a higher TMA value than gutted haddock. The reverse is a possibility.

Samples from Commercial Trawlers

Three round and three gutted haddock were taken at random from each of 13 different landings of three Newfoundland trawlers. The skinned fillets, after the usual trimming, were analysed for TMA content either immediately or after a few days preservation in a deep-freeze at –18°C.

On all the trips from which these haddock were taken, except for one in which only the daily totals are available, a record was kept of the amounts of round and of gutted haddock put down each day. It has, therefore, been possible to calculate the average number of days between catching and sampling that the round and the gutted haddock had been in ice in the hold (Table III). This Table also shows the greatest and the least number of days that could have elapsed for any individual haddock between capture and selection for TMA examination, and also the range and averages of TMA values.

Table IV shows the frequencies of TMA values of the fillets of the 39 round and the 39 gutted haddock from the 13 samples and trawler trips. The two frequencies resemble each other fairly closely, especially in their lower ranges.

TABLE II. Trimethylamine (TMA) values (mg. TMA nitrogen per 100 g. of fillet) of fillets of round and gutted haddock from *Investigator II* samples, 1954 to 1955.

Location of samples	No. days in ice before filleting	No. of haddock		Length of haddock: Range		Length of haddock: Average		TMA values: Range		TMA values: Average		Standard deviation of averages		"t" value	Probability
		Round	Gutted	Round	Gutted	Round	Gutted	Round	Gutted	Round	Gutted	Round	Gutted		
				cm.	*cm.*	*cm.*	*cm.*								
A. Grand Bank, June 4–7, 1954	6	5	5	...	...	...	...	0.46–0.57	0.25–0.50	0.53	0.35	0.04	0.09	4.09	<0.01
	5	5	5	...	...	...	...	0.33–0.64	0.26–0.55	0.47	0.37	0.13	0.11	1.32	>0.20
	3	5	5	...	...	...	...	0.19–0.55	0.19–0.35	0.31	0.31	0.14	0.07		
B. Grand Bank, May 17–22, 1955	9	5	5	41–46	40–48	44	44	0.50–0.82	0.55–2.86	0.69	1.37	0.16	0.90	1.66	>0.10
	7	5	5	40–41	40–41	41	40	0.48–1.09	0.51–0.93	0.73	0.66	0.27	0.16	0.50	>0.60
	4	3	3	40–41	40	41	40	0.48–0.58	0.39–1.06	0.52	0.70	0.05	0.29	1.35	>0.20
C. St. Pierre, Bank, June 14–18, 1955	8	5	5	40–42	41–45	41	42	0.44–1.05	0.73–2.22	0.89	1.57	0.25	0.57	2.45	<0.05
	6	5	5	40	40	40	40	0.74–1.22	0.50–0.78	0.97	0.66	0.18	0.10	3.37	<0.01
	4	5	5	40	40	40	40	0.41–1.41	0.29–0.98	0.70	0.54	0.42	0.26	0.72	0.50
Totals for A+B+C	3	5	5	...	...	...	...	0.19–0.55	0.19–0.35	0.31	0.31	0.14	0.07		
	4	8	10	40–41	40	40	40	0.41–1.41	0.29–1.06	0.63	0.62	0.33	0.28	0.07	>0.90
	5–7	20	20	...	...	...	...	0.33–1.22	0.25–0.93	0.68	0.51	0.26	0.09	2.74	<0.01
	8–9	10	10	40–46	40–48	42	43	0.44–1.05	0.55–2.86	0.79	1.47	0.22	0.72	2.86	0.01

TABLE III. Trimethylamine (TMA) values of fillets of haddock from commercial samples, 1954. (For trip No. 4 round and gutted were not recorded separately per day.)

Trip No.	Fishing dates	Range of number of days between catching and sampling of individual fish		Average number of days between catching and sampling		Range of TMA values of fillets of three fish		Average TMA values of fillets of three fish	
		Round	Gutted	Round	Gutted	Round	Gutted	Round	Gutted
1	Apr. 7–13	2–7	2–7	2.9	4.1	0.10–0.83	0.14–0.61	0.38	0.40
2	Apr. 13–21	2–8	2–8	4.0	2.9	0.47–0.94	0.28–0.40	0.67	0.36
3	Apr. 17–24	5–9	5–9	6.2	6.6	0.68–1.52	0.68–1.11	0.98	0.82
4	Apr. 21–27	3–8		3.9		2.17–3.67	1.52–2.05	3.04	1.82
5	May 6–11	4–6	2–6	3.6	4.9	0.66–2.59	0.40–0.53	1.83	0.49
6	May 9–17	3–9	2–9	5.7	4.9	0.34–1.73	1.09–2.37	0.98	1.84
7	May 15–19	2–5	2–5	3.1	4.7	0.30–1.69	0.39–0.63	0.77	0.55
8	May 30–June 6	2–6	2–6	3.7	2.9	0.34–0.58	0.40–0.82	0.45	0.58
9	Aug. 14–21	3	3–6	3.0	4.0	0.32–6.05	0.23–1.21	2.39	0.69
10	Aug. 25–Sept. 1	3	3–6	3.0	4.8	0.48–1.72	1.86–4.45	1.28	2.73
11	Sept. 1–6	2–4	2–5	3.3	4.0	0.37–8.69	0.49–1.07	3.29	0.87
12	Sept. 4–10	2–6	2–6	3.5	4.2	0.62–1.37	3.49–10.09	1.03	6.50
13	Sept. 18–25	3–6	3	4.9	3.0	0.77–1.10	2.17–4.86	0.95	3.14
Total	Apr. 7–Sept. 25	2–9	2–9	3.9	4.3	0.10–8.69	0.14–10.09	1.38	1.60

TABLE IV. Trimethylamine (TMA) values of fillets of individual round and gutted haddock from the *Investigator II* and from commercial trawlers, 1954 to 1955. (In the *Investigator II* samples, only TMA values from samples with equal numbers of round and gutted haddock were used here. The values for the unequal 4-day sample from the Grand Bank (see Table II) have been omitted. The commercial samples were all of the same number of round and gutted haddock collected from the same trawler at the same time.)

Haddock from *Investigator II*			Haddock from commercial trawlers		
TMA value	No. of samples of round haddock	No. of samples of gutted haddock	TMA value	No. of samples of round haddock	No. of samples of gutted haddock
0.11–0.20	1	1	0.01–0.20	1	1
0.21–0.30	2	3	0.21–0.40	7	7
0.31–0.40	3	10	0.41–0.60	5	5
0.41–0.50	8	5	0.61–0.80	6	6
0.51–0.60	8	5	0.81–1.00	5	1
0.61–0.70	3	3	1.01–1.20	2	4
0.71–0.80	3	4	1.21–1.40	1	1
0.81–0.90	1	0	1.41–1.60	1	1
0.91–1.00	6	2	1.61–1.80	4	0
1.01–1.10	3	0	1.81–2.00	0	3
1.11–1.20	0	0	2.01–2.20	1	3
1.21–1.30	1	0	2.21–2.40	1	2
1.31–1.40	0	2	2.41–2.60	1	0
1.41–1.50	1	1	3.21–3.40	1	0
1.51–1.60	0	1	3.41–3.60	0	1
			3.61–3.80	1	0
1.91–2.00	0	1	4.41–4.60	0	1
			4.81–5.00	0	1
2.21–2.30	0	1	5.81–6.00	..	1
			6.01–6.20	1	0
2.81–2.90	0	1	8.61–8.80	1	0
			10.01–10.20	0	1
Total	40	40		39	39
Mean	0.66	0.73		1.39	1.61
Standard deviation	0.29	0.59		1.67	1.93
"t" value	0.67			0.54	
Probability	0.50			>0.50	

Almost all the TMA values were below 2.5. Judging by the length of the trips and the lower results from the careful icing of the *Investigator II* samples the few high TMA values between 5.9 and 10.2 (one round and three gutted) doubtless resulted from inadequate icing.

The average TMA value for gutted was 1.61 and for round 1.39. As in the *Investigator II* averages the value for round is lower than that for gutted but, here also, the difference between the averages is not statistically significant. The average post-mortem ages of the round and of the gutted haddock in the catches from which the samples were taken were 3.9 and 4.3 days respectively.

Liver Burn and Firmness of Fillet

Liver "burn" is the effect produced on the muscular body wall by the breakdown of the liver in round fish and is presumably autolysis first of the liver and then of the adjacent flesh by the liver enzymes. A liver stain is also likely to be produced in such instances.

Fresh fish processors mention liver burn as one of the disadvantages of landing round haddock after a long period of storage in ice.

Although liver burn was not especially investigated, the haddock fillets of the *Investigator II* samples were examined for damage by liver breakdown, but no very significant damage to the fillet portion of the fish was observed in these carefully iced samples up to the 8- and 9-day periods of storage in ice which formed the limits of these samples.

In these *Investigator II* samples the part of the fillet nearest the belly was sometimes softer in the round than in the gutted fish.

Colour of Fillets

Templeman and Pitt (1954) showed that in the American plaice, *Hippoglossoides platessoides* (Fabricius), whole fish had a much greater amount of bruises or blood spots than fish which were gutted.

In the round haddock from the *Investigator II* samples, which were examined closely, bruising and occurrence of reddening under the skin did not appear to be serious enough to affect the marketability of the product. The fillet from the round haddock, however, is a little darker than that from gutted haddock, but not objectionably so. This whiter colour of the fillet of the gutted haddock is due to the drainage of blood from the gutted fish and further leaching of blood from the exposed body cavity in the iced, gutted fish. Fresh fish processors are also aware of the slightly darker colour of the fillets of round haddock. The additional reddening below the skin of the fillet from the round fish is not a serious matter since haddock fillets are usually sold without removing the skin.

In comparison, in frequent landings of round cod at the Station by the *Investigator II* since 1946, we have found fillets from these round otter-trawler cod to be in an excellently fresh condition when well iced, up to over a week after capture. However, otter-trawler cod, especially the larger fish, are usually very red in colour under the skin if landed iced in the round condition. It may be that cod have a greater blood supply under the skin. Also, since cod are, on

the average, larger and much more vigorous than haddock, they can probably be bruised or can bruise themselves more than haddock after capture.

DISCUSSION AND CONCLUSIONS

The foregoing experiments and observations show no difference in freshness, judged by TMA values, between gutted and round haddock.

Castell and MacCallum (1953) showed that for the American plaice, *Hippoglossoides platessoides* (Fabricius), when the fish were well iced, the fillets from the gutted and ungutted flounders were indistinguishable up to 4 days. From the fourth to the seventh day, however, the ungutted flounders deteriorated faster than the gutted fish. There were no significant differences in bacterial counts or TMA values for freshly cut fillets from gutted or ungutted flounders up to 7 days in ice. Softening and liver stains contributed to the inferior condition of the ungutted fish after the fourth day.

All the haddock landed in Newfoundland from trawlers are filleted and the fillets frozen soon after landing. The problem is, therefore, one of keeping the fish in good condition up to the time of freezing.

In the summer-time the usual custom on the commercial ships is either to keep the trips of only a few days duration, which is possible if the haddock are very plentiful, or to fish other species and to put down round haddock only during the last 3 days of trawling. In the winter and spring it is apparently possible to land round haddock in acceptable condition after a week of fishing.

Although in our tests the gutted and round haddock showed no differences in freshness, the gutted haddock in these experiments and observations were iced down after a relatively short period on deck. With the very large commercial hauls of ten to twenty thousand pounds per haul, which were common in the years when fish of the 1949 year-class of haddock were most plentiful, undoubtedly, if in the summer-time all these small haddock had been gutted, the resulting condition of freshness would have been inferior to that of fish put below immediately and iced in the round condition.

The excellent results and narrow range of TMA values in the *Investigator II* experiments and the occasional high individual TMA values from the commercial boats indicate that the commercial boats in the summer-time should ice their round fish very adequately and carefully.

In spite of the evidences in this paper showing little difference in the quality of fillets from round and from gutted haddock, both when adequately iced experimentally and under ordinary short-trip commercial conditions, there are many questions concerning the relative quality of these products which need to be approached by means other than determination of TMA values.

ACKNOWLEDGMENTS

We are extremely grateful to the St. John's Fish Inspection Laboratory of the Federal Department of Fisheries and to Mr. John P. Hennessey, chief of the laboratory, for carrying out the trimethylamine determinations used in this paper. Mr. V. M. Hodder has read the paper and we are grateful for his suggestions.

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A Preliminary Study of the Feeding Habits of the Japanese Oyster Drill, *Ocinebra japonica*[1,2,3]

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ABSTRACT

Individually marked Japanese oyster drills, *Ocinebra japonica*, were presented with a choice of four different food organisms: mussels (*Mytilus edulis*); clams (*Venerupis japonica*); and oysters (*Crassostrea gigas* and *Ostrea lurida*). During the course of the 65-day experiment, mussels constituted 42.6 per cent of the food organisms attacked by drills; clams, 36.5 per cent; and oysters, 20.9 per cent. The average time that an *Ocinebra* took to drill through a shell and finish feeding on the body mass are: mussels, 4.98 days; clams, 6.31 days; Olympia oysters, 5.70 days; and Pacific oysters, 14.0 days (on the basis of one Pacific oyster). Experimental evidence suggests that a drill will continue to attack the same species of food organism that it had attacked previously, rather than moving to an easily accessible organism of a different species.

INTRODUCTION

The Japanese drill, *Ocinebra japonica* Dunker, is considered by oyster growers of the Pacific coast to be potentially the most serious predator on both species of cultivated oysters, *Crassostrea gigas* and *Ostrea lurida*. It has been stated that the Japanese drill has been found to drill oysters, with resultant damage to the oyster stocks [1, 2].

There is little information on the preference of *Ocinebra* for the organisms that it is known to attack. Chapman and Banner [3], in the only article upon this subject, reported that the *Ocinebra* attacks Olympia oysters in preference to mussels and barnacles.

To ascertain whether the Japanese drill exhibits a discriminatory behaviour in its choice of food when confronted with four different species of bivalves (Manila clam, *Venerupis japonica*; bay mussel, *Mytilus edulis*; Olympia oyster, *Ostrea lurida*; Pacific oyster, *Crassostrea gigas*), a study was conducted (April 11, 1957 to June 13, 1957) at the University of Washington, College of Fisheries.

MATERIALS AND METHODS

The test animals used in the study were obtained from three sources: the mussels and Pacific oysters from Poulsbo (Liberty Bay), Washington; the clams and Olympia oysters from Point Whitney (Hood Canal), Washington; and the drills from Oyster Bay (Southern Puget Sound), Washington.

The food organisms were selected randomly in the field. The lengths of all food organisms were measured between the most anterior and posterior points on the valves. The size ranges of these organisms were as follows: Manila clam, 33–37 mm.; Bay mussel, 35–43 mm.; Olympia oyster, 32–42 mm.; and Pacific

[1]Received for publication November 6, 1957.

[2]Contribution No. 31, College of Fisheries, University of Washington, Seattle, Washington.

[3]The generic name formerly used for this drill is *Tritonalia*: Minutes 149 (August 1955), Conchological Club of Southern California.

J. Fish. Res. Bd. Canada, 15(4), pp. 529–535, 1958.
Printed in Canada.

oyster, 40–50 mm. All of the experimental animals, except the Pacific oysters, were adults.

The drills were collected from two of their food sources; namely, the Olympia oysters and Pacific oysters. The drills were kept separate and were tested separately. The size range of the drills used in this experiment was from 33–42 mm. (tip of siphonal canal to apex). Individual drills were marked for identification with synthetic paint (Speedtec Synthetic Finish, Fuller Paint Co., Seattle, Washington). One colour was painted on the apex, and another colour on the varices.

Two separate aquaria were used for this study; one to test the drills collected from Olympia oysters, and the other to test the drills from Pacific oysters. Each aquarium measured 61 cm. wide, 140 cm. long and 66 cm. high. The inflow and outflow of water were near opposite ends of the tank, approximately 132 cm. apart. The water level in these aquaria was maintained at 40 cm. Sea-water from Puget Sound was recirculated through the aquaria at the rate of about one litre per minute. Throughout the test period the water temperature was maintained at 10.6°C. (±0.30°C.). A 100-watt light bulb over each aquarium was turned on every morning and off every evening. This was done to simulate day- and night-time conditions. There were approximately 9–10 hours of light and 14–15 hours of darkness.

The marked drills were conditioned to the salt water of the circulating system of the aquaria for 11 days before the experiment was started, during which time they were not fed. After the acclimatizing period, the marked drills were placed in the two tanks where the four kinds of prey were distributed (see Fig. 1). All

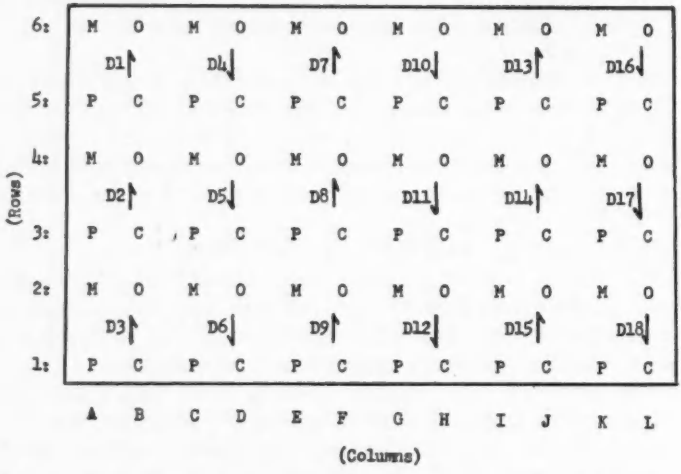
6: M O M O M O M O M O M O
D1 D4 D7 D10 D13 D16
5: P C P C P C P C P C P C
4: M O M O M O M O M O M O
D2 D5 D8 D11 D14 D17
3: P C P C P C P C P C P C
2: M O M O M O M O M O M O
D3 D6 D9 D12 D15 D18
1: P C P C P C P C P C P C
(Rows)
A B C D E F G H I J K L
(Columns)

FIG. 1. Arrangement of food organisms on bottom of aquarium, and position of each drill at time of release.

M: Bay mussels.
O: Olympia oysters.
P: Pacific oysters.
C: Manila clams.
D+Arabic numerals: Japanese drills.
↑↓ Initial orientation of siphonal canal.

drills were released with the siphonal canals pointing in the direction as shown in the Figure. The food organisms were arranged in such a pattern that each drill had an equal opportunity to attack one of the four species. Even if a drill moved from one square to another, the same choice of food organisms was offered.

Observations of drills were made daily between 5:00 to 7:00 p.m. The location of each drill and the animal being attacked were noted and tabulated. For example, it was noted that a drill was attacking C4–M food animal. Referring to the Figure, the C represents Column C, the 4 represents row 4, and the M represents the mussel. This method of noting locations of drills made it possible to keep an accurate record of the food animals attacked by drills and the duration of attack.

When a food organism had been drilled and eaten, it was removed and replaced by another animal of the same species. The credit for this mortality then was given to the drill previously noted on the dead organism. If two drills attacked the same organism, credit was given to the drill that arrived first on the food animal.

RESULTS

A summary of the major observations is presented in Tables I and II. In these tables, column A represents the species of food animal attacked (C—clam, M—mussel, O—Olympia oyster, and P—Pacific oyster); column B represents the location; and column C represents the number of days the drill remained on the victim.

Statistical (chi-square) tests (Table III) did not reveal any significant difference between the number or type of organisms attacked by drills collected from either Pacific or Olympia oysters; accordingly, the data from Tables I and II were combined.

TABLE I. Summary of observations of drills collected from Olympia oysters. A: species attacked; B: location; C: duration of attack in days.

Drill number	1st attack A B C	2nd attack A B C	3rd attack A B C	4th attack A B C	5th attack A B C	6th attack A B C
1	C–H5–9	C–J3–7	C–J5–7	C–H3–5		
2	O–H4–7	O–J6–8	O–J6–5	O–D6–6	O–D2–5	
3	M–A4–6	M–C6–5	M–E2–8	M–I2–5		
4	Dead					
5	...					
6	M–C4–5	M–A6–4	M–C6–6	M–E4–5	M–K6–4	
7	Dead					
8	C–D5–4					
9	M–C2–8	M–A6–4	M–A6–2	M–E2–3	M–E4–3	M–K4–3
10	C–D3–2	C–H1–8				
11	C–L5–8	C–L1–8	C–J1–4	C–J3–7	C–J1–6	C–D1–6
12	M–I6–6					
13	C–F3–10	C–F5–8	C–B5–3	C–F3–9	C–J1–3	
14	M–K4–5	M–K6–7	M–I6–6	M–K2–5		
15	O–F4–6	O–L6–9				
16	C–F5–9	C–B1–9	O–B4–11	O–D6–5	O–B4–7	
17	M–G6–6	M–E6–7	C–J5–4			
18	O–D2–5	C–B1–6				

TABLE II. Summary of observations of drills collected from Pacific oysters. A, species attacked; B, location; C, duration of attack in days.

Drill number	1st attack A B C	2nd attack A B C	3rd attack A B C	4th attack A B C	5th attack A B C	6th attack A B C
1	O–H6–5	M–A6–1	C–B1–2			
2	...					
3	M–C6–4	M–A4–3				
4	C–B3–6	C–H5–7	C–D1–5	C–B5–6		
5	O–F4–8	O–H6–6				
6	M–C6–7	M–E6–6	M–A6–4	M–C6–4		
7	C–B3–7	C–D3–8	C–L5–6	C–L1–9		
8	M–A6–2	M–A2–7	M–E6–8	M–G2–5	M–I4–6	
9	M–A6–5	M–G6–4	M–A4–4	M–C4–4		
10	M–C2–6	M–I6–6	M–G4–5	M–G6–7	M–E2–3	
11	O–L2–3	C–H1–8	O–L6–1	C–L5–6	C–B5–5	C–H1–6
12	P–K3–14	O–F4–2	O–H2–4	O–H4–7	O–H2–7	
13	M–G2–1	M–C2–7	M–E2–6			
14	C–L3–9	C–D1–4	C–D5–6	C–B1–7	C–F3–3	C–D1–6
15	O–H2–6	O–D6–5	C–F5–7			
16	O–B2–3					
17	...					
18	M–G4–5	M–G6–7	M–K6–6			

TABLE III. Chi-square test on the number or type of organisms attacked by drills in both aquaria. Aquarium 1, drills collected from Pacific oysters; Aquarium 2, drills collected from Olympia oysters.

	Aquarium 1 (observed)	Aquarium 2 (observed)	Aquarium 1 (expected)	Aquarium 2 (expected)	Totals
Bay Mussel	27	22	25.57	23.43	49
Manila Clam	20	22	21.91	20.09	42
Olympia Oyster	12	11	12.00	11.00	23
Pacific Oyster	1	0	0.52	0.48	1
Totals	60	55	60.00	55.00	115

Chi-square value of 1.44, with 3 degrees of freedom.

Table IV represents the combined data and shows the number of food organisms attacked by the drills and the duration of attack. The average number of days taken by the drills to bore through a shell and consume the soft parts is as follows: mussels, 4.98 days; clams, 6.31 days; Olympia oysters, 5.70 days; and Pacific oysters, 14.0 days (on the basis of one Pacific oyster).

During the course of the 65-day experiment the number of organisms attacked by any one drill ranged from zero to six, with a mean of 3.4 organisms.

Under the conditions of this experiment, it was found that mussels constituted 42.6 per cent of the food organisms attacked; clams, 36.5 per cent; Olympia oysters, 20.0 per cent; and Pacific oysters, 0.9 per cent.

DISCUSSION

No study has been made on the feeding processes of the *Ocinebra*. However, because of the close systematic position of *Ocinebra* to *Urosalpinx*, it is highly probable that their feeding processes are similar. According to Carriker [4],

TABLE IV. Number of organisms attacked and duration of attack in days. A: number of organisms attacked; B: total days of attack; C: average days of attack.

	1st attack A B C	2nd attack A B C	3rd attack A B C	4th attack A B C	5th attack A B C	6th attack A B C	All attacks A B C
Bay mussel (M)	13–66–5.08	13–68–5.23	10–55–5.50	8–38–4.75	4–16–4.00	1– 3–3.00	49–244–4.98
Manila clam (C)	9–64–7.00	10–73–7.30	9–44–4.88	7–49–7.00	4–17–4.25	3–18–6.00	42–265–6.31
Olympia oyster (O)	8–43–5.38	5–30–6.00	4–21–5.25	3–18–6.00	3–19–6.33	0	23–131–5.70
Pacific oyster (P)	1–14–14.00	0	0	0	0	0	1– 14–14.00

Urosalpinx cinerea (Say) has a feeding process which consists of mechanical rasping of the softer flesh of the prey. The proboscis is extended through the newly drilled hole and the radula tears away bits of flesh with its sharp, backward-pointed teeth. Flesh caught on the radular teeth and transported into the buccal cavity is neatly removed by oesophageal suction and then carried by ciliary peristaltic activity to the stomach.

In the present experiment it was found that when a hole had been drilled through a mussel or a clam, the soft parts of the visceral mass were gone, leaving intact the harder parts such as the siphon (absent in mussels), mantle edges, foot, and parts of the adductor muscles. Usually, only fragments of the adductor muscles were left in oysters. Whether or not these remaining parts would have been eventually consumed is unknown for, whenever a drill hole perforated a shell completely, the food animal was considered dead and was replaced by another of the same species. A dead organism was replaced only during the time when observations were made, and after the drill had left this prey. Carriker [4] points out that the radula of the *Urosalpinx* is ineffective in rasping tissues such as the adductor muscles of adult oysters until partial autolysis has taken place. It is possible that the cool temperature (10.6°C.) in the two experimental tanks may have delayed normal autolytic action on the hard parts of the visceral mass of drilled bivalves. The *Ocinebra* may have been discouraged by this delay, and subsequently left the hard parts of the visceral mass partially or wholly intact in the bivalves.

Since the drills were collected from Pacific and Olympia oysters, it might be expected that the percentage of attack would be greatest upon these two species of oysters. This was not the case. The two species of oysters constituted only 20.9 per cent of the organisms attacked. The food animal consumed in greatest numbers by the *Ocinebra* was the bay mussel. This experiment suggests that the Japanese drill may prefer mussels to the three other species of bivalves. Contrary to this, Chapman and Banner [3] reported that the *Ocinebra* attacks Olympia oysters in preference to mussels and barnacles. In their experiment, Chapman and Banner placed varying numbers of Olympia oysters, mussels, barnacles, and Japanese drills in one-gallon aquaria equipped with running water. The organisms were left for approximately one month and the contents were examined at the end of this period for drill holes.

The precise mechanism by which the Japanese drill differentiates between species of prey is unknown, and remains to be adequately studied. Frederighi [5] points out that, as in nearly all other marine molluscs, the *Urosalpinx* possesses an osphradium—an organ intimately connected with the breathing organs and generally near their base. The *Urosalpinx* is undoubtedly attracted to the food through the osphradium. Whether or not this applies to the *Ocinebra* is unknown.

There were 84 possible chances (total possible pairs of attacks in Tables I and II) for the drill to attack the same species that it had attacked previously. Of the 84 possible pairs of attacks, 74 pairs were attacks on the same species. This indicates that a drill will usually continue to attack the same species of food organism that it has attacked previously.

It was observed that some drills deposited egg cases in the early days of this experiment. These egg cases were cemented on the shells of several Pacific oysters, and on the bottoms and sides of both aquaria. It was interesting to note that no egg cases were found on any other test animal except Pacific oysters, indicating that the Japanese drill may be able to differentiate between species of bivalves.

SUMMARY

1. Individually marked Japanese drills, collected from either Pacific oysters or Olympia oysters, were presented with a choice of four different food organisms: bay mussels (*Mytilus edulis*); Manila clams (*Venerupis japonica*); Pacific oysters (*Crassostrea gigas*); and Olympia oysters (*Ostrea lurida*).

2. Statistical (chi-square) tests did not reveal any significant difference between the number or type of organisms attacked by drills collected from either Pacific or Olympia oysters.

3. Mussels constituted 42.6 per cent of the food organisms attacked by drills; clams, 36.5 per cent; Olympia oysters, 20.0 per cent; and Pacific oysters, 0.9 per cent.

4. The average time that an *Ocinebra* took to drill through a shell and finish feeding on the body mass are: mussels, 4.98 days; clams, 6.31 days; Olympia oysters, 5.70 days; and Pacific oysters, 14.0 days (on the basis of one Pacific oyster).

5. During the course of the 65-day experiment, the number of organisms attacked by any one drill ranged from zero to six, with a mean of 3.4 organisms.

6. It was found that whenever a hole had been drilled through a mussel or a clam, the soft parts of the visceral mass were gone, leaving the harder parts. Usually, only fragments of the adductor muscles were left in oysters.

7. Experimental evidence suggests that a drill will continue to attack the same species of food organism that it had attacked previously, rather than moving to an easily accessible organism of a different species.

8. Early in this experiment, several drills deposited egg cases on Pacific oysters, but none were deposited on any of the three other food organisms. This suggests a possibility that the Japanese drills are able to differentiate between species of bivalves.

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The Effect of Various Lighting Conditions on the Efficiency of "Candling" Cod Fillets for Detection of Parasites[1]

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ABSTRACT

The efficiency of candling cod fillets was studied using various values and colours of light transmitted through the cod flesh and various values of incident light. It was found that there was no advantage gained in using other than white light for transmission through the fillet. It was also found that a low level of incident light was desirable if the maximum number of parasites is to be detected.

The codfish, along with several other species of fish, sometimes suffers from an infection by the larvae of a nematode parasite of marine mammals. This nematode, commonly but erroneously called the codworm, belongs to the species *Porrocaecum (Terranova) decipiens.*

In recent years the problem of detecting and removing parasites from cod fillets has become one of prime importance to the Atlantic coast fishing industry. Although several methods for detection and removal of parasites have been suggested, the only one which has shown itself to be commercially feasible is that of "candling", i.e. visual examination of the fillet with a light source placed under the fillet, and removal of the parasites, individually, by hand.

In candling the flesh of whitefish from lakes of the central provinces of Canada for larvae of *Triaenophorus crassus*, McMurtrie and Carter (1948) showed that there was no advantage in using other than white light. This also proves to be the case in candling Atlantic cod.

The present experiment was conducted to determine the effects of a number of factors on the efficiency with which cod fillets could be candled and the parasites removed. The factors studied were intensity and colour of the light under the fillet (transmitted light) and the intensity of the light falling on the surface of the fillet (incident light). The room light or incident light was varied from 0 to 100 foot-candles.

A small, one-man candling table with a 12- by 24-inch (30- by 60-cm.) glass top was built for use in these tests. It was equipped with three frosted 150-watt incandescent light bulbs located 8 inches (20 cm.) below the glass inspection surface. When a blue filter was used, it was necessary to increase the illumination source to six 200-watt bulbs to obtain sufficient transmitted light. The light output of these bulbs could be varied from zero to maximum by means of a 1,000-volt-ampere variable voltage autotransformer having a voltage output which could be infinitely varied between 0 and 135 volts.

A series of filters was made up. Each was 12 inches wide by 24 inches long to fit the top of the candling table; the filter used for white light was opal glass,

[1]Received for publication December 26, 1957.

J. Fish. Res. Bd. Canada, 15(4), pp. 537–542, 1958.
Printed in Canada.

while the green, blue, yellow, and red filters were made from translucent coloured acrylic plastic ⅛ inch (3 mm.) thick. The density–wavelength curves for these filters are shown in Fig. 1.

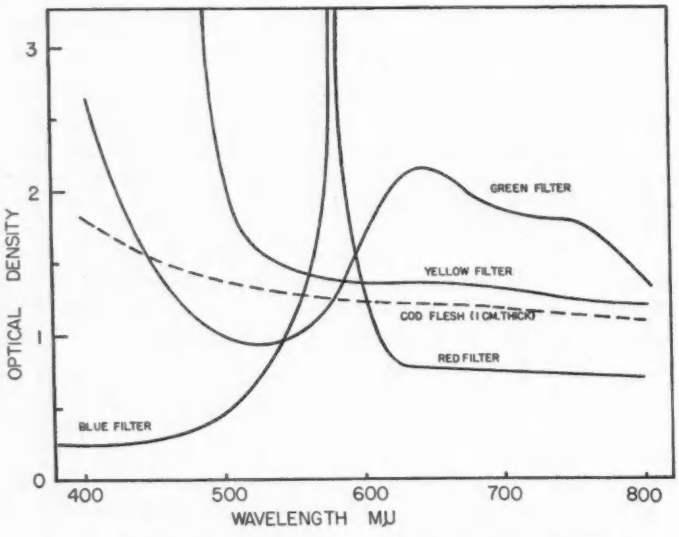

FIG. 1. Optical density curve for the various filters used for candling cod fillets and for cod flesh 1 cm. (⅜ inch) thick.

Above the table a 500-watt R-2 Photoflood bulb was mounted to illuminate the surface of the table and provide a variable source of incident light. This bulb also could be supplied with voltage varying between 0 and 135 volts from a 1,000-volt-ampere variable voltage autotransformer. A schematic drawing of this set-up is shown in Fig. 2.

To measure the light transmitted through the candling surface and also the amount of incident light falling on the surface, a Weston Photronic Foot-Candle Meter, Model 614 (Weston Electrical Instrument Corp., Newark 5, N.J., U.S.A.) was used. This instrument is equipped with a visual correction filter for colour and so has the same colour response to coloured light as has the human eye. The relative spectral sensitivity of this meter is shown in Fig. 3, together with the sensitivity curve for the human eye.

This curve shows how closely the response curve of the light meter follows the response curve for the human eye, ensuring that the light values used in candling these cod fillets were varied in accordance with the response of the human eye to the different coloured filters used.

During the experiment 245 medium-sized cod fillets were examined. In size the fillets were representative of a normal commercial pack. The maximum thickness of these fillets varied between the limits 0.5 and 1.25 inch (1.3 to 3.2 cm.);

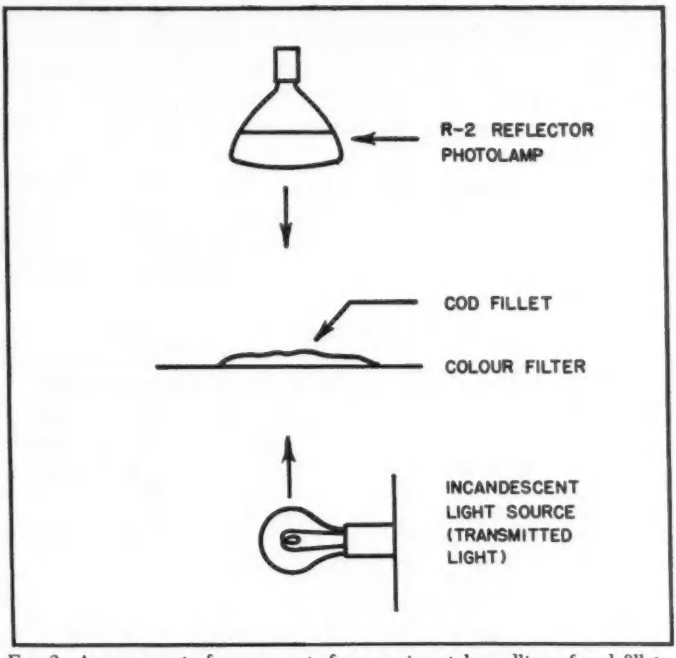

FIG. 2. Arrangement of components for experimental candling of cod fillets.

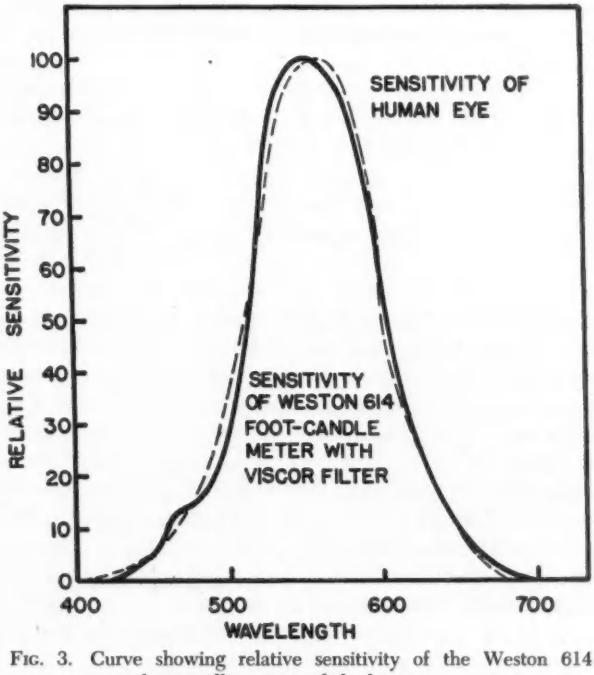

FIG. 3. Curve showing relative sensitivity of the Weston 614 foot-candle meter and the human eye.

the length varied between the limits 11.5 and 20 inches (29 to 51 cm.). From these fillets 1,896 parasites were removed. The average parasite content of each fillet was 7.7. For each curve obtained an average of 12.9 cod fillets were examined.

The approximate wattages required at 115 volts to obtain a desired level of transmitted light through a 12- by 24-inch opal glass candling surface are shown in Table I. The light measurements were taken 7 inches (18 cm.) to the left of centre, at the centre, and 7 inches to the right of centre, at the candling surface.

TABLE I. Wattages required to give various values of transmitted light.

Light source	Number and specification of bulbs		Average transmitted light intensity	Distribution of light		
				Left	Centre	Right
total watts			*foot-candles*		*foot-candles*	
200	1	200-watt	330	310	370	310
150	1	150-watt	280	200	360	200
80	2	40-watt	177	180	175	175
75	3	25-watt	160	150	180	150
50	2	25-watt	97	90	100	100
40	1	40-watt	85	65	120	70
25	1	25-watt	57	45	80	45

The lamps were placed 8 inches below the level of the opal glass in a horizontal plane. When one lamp was used it was placed in the centre of the 24-inch length of the candling surface. When two lamps were used, they were in sockets 7 inches on either side of the centre line. When three lamps were used, all three positions were used.

The procedure used to determine the effect of colour and intensity of light on the efficiency with which codworms can be detected in cod fillets was as follows. The incident light was adjusted by means of the variable voltage supply to give the desired light intensity, measured in foot-candles, on the surface of the table. This remained constant while each fillet was examined at transmitted light levels of 0, 5, 10, 50, 100, 200, and 300 foot-candles. At each level of light all the visible parasites were removed and their number was recorded. The transmitted light was then increased to the next level, the fillets were re-examined, and any additional visible parasites were removed and recorded. After the fillets were examined at the 300-foot-candle level, they were then shredded with a knife, and the number of residual parasites that had escaped detection was recorded.

The above procedure was repeated at incident light levels of 0, 10, 50, and 100 foot-candles with white, green, blue, yellow, and red filters on the candling surface.

The results given in this paper are useful for comparison only, and it is doubtful that these values could be approached under commercial conditions.

The numbers of residual parasites were calculated as percentages of the total numbers of parasites; these values were then plotted against the intensity of the transmitted light. The resulting curves are shown in Fig. 4, 5, 6, and 7. In general it may be seen from the curves that with no incident light, the

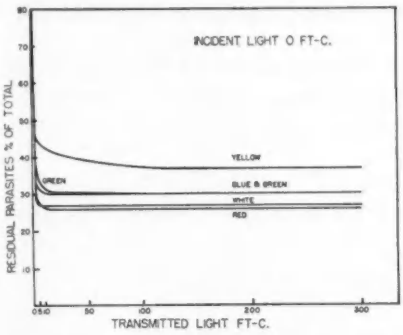

FIG. 4. Curves showing the effect on candling of various values of transmitted light with coloured filters at 0 foot-candles of incident light.

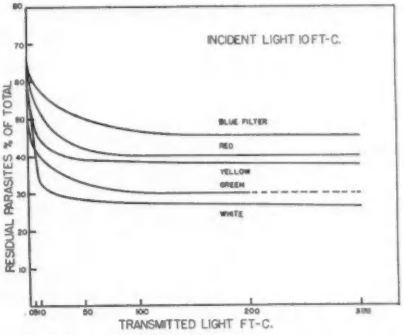

FIG. 5. Curves showing the effect on candling of various values of transmitted light with coloured filters at 10 foot-candles of incident light.

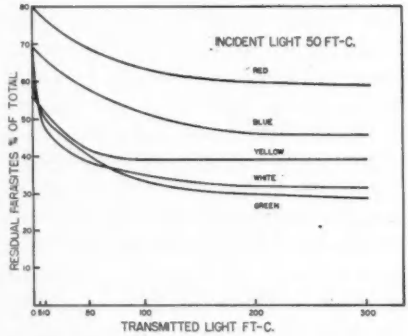

FIG. 6. Curves showing the effect on candling of various values of transmitted light with coloured filters at 50 foot-candles of incident light.

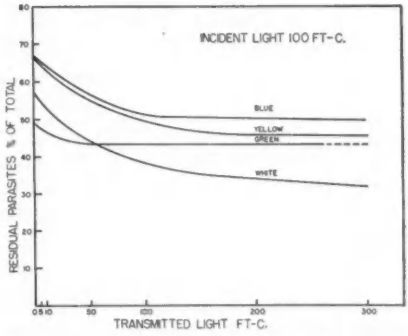

FIG. 7. Curves showing the effect on candling of various values of transmitted light with coloured filters at 100 foot-candles of incident light.

percentage of residual parasites drops very quickly and then levels off and remains constant for all colour filters. As the incident light level is raised, the percentage of residual parasites drops more and more gradually and a much higher level of transmitted light is required for this percentage to reach its minimum value.

With an incident light value of zero, that is, in a darkened room (Fig. 4), the red and white light gave the lowest percentage of residual parasites in the cod fillets. Under these conditions, and with very careful candling, all but 26 to 27% of the parasites could be removed. Other coloured filters gave poorer results, the blue and green allowing 30%, and the yellow 37%, of the parasites to remain undetected. However, candling in a darkened room, especially with the red filter, proved very tiring to the eyes.

With the room lighting raised to 10 foot-candles, a higher level of transmitted light was needed to detect parasites in the fillet as shown in Fig. 5.

In this case white light proved to be the better choice for candling. As the incident light value is increased to 50 foot-candles, the candling operation becomes less efficient. White and green coloured filters are the best for use in candling cod fillets at this level.

At an incident light value of 100 foot-candles, the efficiency of candling becomes even lower. The white and green filters gave the best results. These results are recorded in Table II.

TABLE II. Residual parasites at various incident light values with coloured filters at a transmitted light level of 300 foot-candles.

Colour of filter	Incident light values (foot-candles)			
	0	10	50	100
	percentage of residual parasites			
White	26.2	27.0	31.5	32.0
Green	30.5	30.0	29.5*	43.5*
Yellow	37.0	37.5	39.0	45.5
Red	26.0	40.0	58.0	...
Blue	30.2	45.5	46.0	50.0

*Extrapolated.

CONCLUSIONS AND OBSERVATIONS

1. Under the best possible conditions we can expect to remove only 73 to 74% of the worms present in heavily infected cod fillets. It was observed during this work that parasites more than ¼ inch (6 mm.) below the surface, or in the brown flesh on the skin side of the fillet, or under the silver bloom, are unlikely to be detected by candling.

2. For practical application, white light is most satisfactory for use in candling tables.

3. Parasite detection is facilitated by reducing the room light intensity in the candling room.

4. The candling surface should be shaded from direct illumination.

5. With a completely darkened room there is little point in using more than 10 foot-candles of transmitted light for candling cod fillets.

6. With the work area illuminated to a level of 10 foot-candles, approximately 50 foot-candles of transmitted light is required.

7. For efficient candling, an incident light value of 3 to 5 foot-candles and a transmitted light value of approximately 50 foot-candles should be used without filter, i.e. white light.

ACKNOWLEDGMENT

The author wishes to thank Dr. W. J. Dyer of this Station for the preparation of the density curves for the filters used in this experiment.

REFERENCE

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Artificial Drying of Salt Fish by Thermocouple Control[1]

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ABSTRACT

In order to provide for ideal conditions of temperature and relative humidity in artificial dryers for salt fish a new method of control has been devised. A thermocouple, inserted in the flesh near the surface, regulates temperature of the air circulating in the dryer. Experiments with light and heavy salted fish confirmed theoretical considerations. The new method increases the drying rate, permits drying under unfavourable atmospheric conditions and avoids over-drying of the surface. Consequently, the difficulty of obtaining uniform batches of choice quality has been minimized. Light salted fish can be dried in three separate periods instead of four.

INTRODUCTION

The artificial drying of salt fish is of comparatively recent origin. Following the investigations of Linton and Wood (1945) on heavily salted fish and of Legendre (1955) on lightly salted codfish, a number of artificial dryers are now in operation for both products. In general, these dryers work very efficiently, but only under favourable atmospheric conditions. During the warm and moist summer months, which is precisely the period when the volume of production is at a maximum, difficulties are encountered; for instance, low drying rate with some sliming as an indirect result. In certain regions artificial drying is even impossible. The installation of a dehumidifying system in conjunction with the artificial dryer would solve this problem from the scientific point of view. However, the cost of this equipment is too high for a cheap nutritional product like salt fish. Therefore other ways and means, which would improve the efficiency of the operation, have been investigated. A system of automatic controls, which continuously maintains optimal conditions of temperature and relative humidity, has been designed, tried and found to give satisfactory results.

GENERAL THEORY OF DRYING

The relative amount of water which is removed during a certain unit of time from a given weight of fish is called the *drying rate* and is usually expressed in pounds/hour. In principle, the process of drying consists of two separate physical phenomena, namely the evaporation of water from the surface and the passage of water from the centre of the semi-solid material towards its surface. Thus, assuming that velocity and distribution of air are uniform, two distinct stages of drying are observed, namely the *constant-rate period* and the *falling-rate period.*

During the *constant-rate period* water travels to the surface of the material at a rapid rate keeping it constantly wet. Consequently evaporation proceeds as if no solid material were present and the product tends to assume a temperature corresponding to the wet bulb temperature of the surrounding air.

[1]Received for publication January 3, 1958.

J. Fish. Res. Bd. Canada, 15(4), pp. 543–554, 1958.
Printed in Canada.

As drying continues, the surface contains less and less water and a condition is reached whereafter moisture evaporates faster than the speed by which it travels to the surface. The *falling-rate period* starts. The moisture content at the dividing point between the two stages is called the *critical moisture content.* Initially the *falling rate* is *constant.* The surface of the material is gradually drying out, the amount of the remaining wet surface decreases and consequently the drying rate is reduced. A phase of "unsaturated-surface drying" takes place.

At the next stage the surface becomes quite dry, and contrary to the mode of moisture transfer during the constant-rate period, water evaporates in the interior parts and passes through the surface in the vapour state. The dried outer portion gradually increases in depth; that is, the zone of moist material recedes more and more towards the interior and consequently the water vapour has a longer way to travel because of the physical obstacle presented by this increasing thickness of the dry outer layer. As a result, subsurface drying proceeds at a *varying falling rate.* This period continues until an equilibrium (between the vapour pressure of the moist material and the vapour pressure of the circulated air) has been reached, which depends mainly on the humidity of the surrounding air. At this point further removal of water from the material is impossible.

During the constant-rate and constant-falling-rate periods the magnitude of the drying rate depends only upon the heat transfer coefficient, which can be calculated from the area exposed to the drying medium and the difference in temperature between the air stream and the wet surface of the solid. These external variables are influenced by temperature, humidity and velocity of the drying air and by the way in which the material is exposed.

In the varying-falling-rate period however, which applies during subsurface drying, the internal mechanism of flow (liquid as well as vapour) is the controlling factor and external variables have only an indirect influence. An increase in temperature raises the rate of fluid flow (capillary and diffusion) whereas the air velocity determines the coefficient of heat transfer between the air and the material. The rate is directly proportional to the free moisture content of the material which is influenced by the humidity of the drying air. However, the material itself, its constitution and especially its thickness, are additional factors of great importance.

ARTIFICIAL DRYING OF SALTED CODFISH

In the drying process of salt fish, because the drying rate is high, the *constant-rate period* is very short. Contrary to this the unsaturated-surface-drying period lasts much longer. This latter period is critical because the surface layer of the material is still moist, therefore perishable and susceptible to bacterial decomposition. This fact is particularly pertinent for light salted fish, which contains more water than heavy salted fish. Therefore the drying through this period should be performed at the highest possible rate.

For a given dryer, operated at a constant air velocity, the drying rate for the first two periods depends only on the difference in temperature between the

air stream and the wet surface of the fish which assumes a temperature corresponding to the wet bulb temperature of the air. This fact conforms to the general theory outlined above. However, we know from psychrometry that for any given initial air condition the difference between the wet and dry bulb temperatures increases with an increase in the temperature of the air. Therefore the best drying rate will be obtained if the highest feasible dry bulb temperature of the air is applied. It could be as high as the boiling point of water, but limitations are set by the liability of fish to be cooked when its temperature exceeds 80°F. (27°C.) (Linton and Wood, 1945; Legendre, 1955).

Subsurface drying requires still more time than unsaturated-surface drying. Here the drying rate is governed by the internal rate of moisture flow, on which temperature and relative humidity of the air have only a limited influence, the composition of the material being the determining factor. In spite of this, the shape of the curve is such that a small increase in drying rate results in an appreciable decrease in drying time. For that reason it is of economic importance to use the most favourable conditions. It must be considered that at this stage of the process the surface is dry, that is, the fish temperature tends to assume the dry bulb temperature of the drying air. Again, the highest permissible temperature for this period, namely the highest temperature which would dry but not cook the fish, was found to be 80°F. The relative humidity of the air has also an important bearing on the surface appearance. If it is too low, the drying process proceeds so fast that a rough surface is formed, which is not acceptable to the trade. It has been found that a relative humidity of 60% is about the lowest which can safely be used with salt fish when its surface is dry (Legendre, 1955). If the relative humidity is lower than 60% it is necessary to increase it artificially to this value.

From the foregoing it is evident that the required conditions of temperature and relative humidity are quite different during the various stages of the drying operation and that they depend upon the state of dryness of the fish surface at each individual instant. As long as the surface is wet (during constant-rate and unsaturated-surface drying), the temperature of the air circulating over the fish must be as high as possible and its relative humidity as low as possible.

When the surface is dry (during subsurface drying), the temperature of the air must be decreased to 80°F., and its relative humidity must be increased to 60%.

Industrial plants usually maintain a constant air temperature of 80°F. The relative humidity is also kept fairly constant, usually at 50 to 55% for the whole drying operation. This compromise, referred to in the following comparative experiments as the "ordinary control" or "conventional control" methods, gives satisfactory results, but only when atmospheric conditions, such as temperature and humidity, are favourable. Because of the limitations of such methods, it was decided to devise a new method of control which would maintain the most favourable conditions during the whole drying operation and to check its performance experimentally.

THERMOCOUPLE CONTROL

A schematic diagram of the new method of control is shown in Fig. 1. The thermocouple sensing element of controller system I is inserted in the fish flesh near the surface and regulates the temperature of the air circulating over the fish in the dryer. The controller is adjusted to 80°F., thus there is no danger of overheating the product. The air is always at the highest permissible temperature. At the beginning of the operation, when the surface of the product is still wet, the temperature of the air will be very high but the temperature of the product will approach the wet bulb temperature of the air because the rapidly proceeding evaporation exerts a cooling effect on the fish. As evaporation proceeds further,

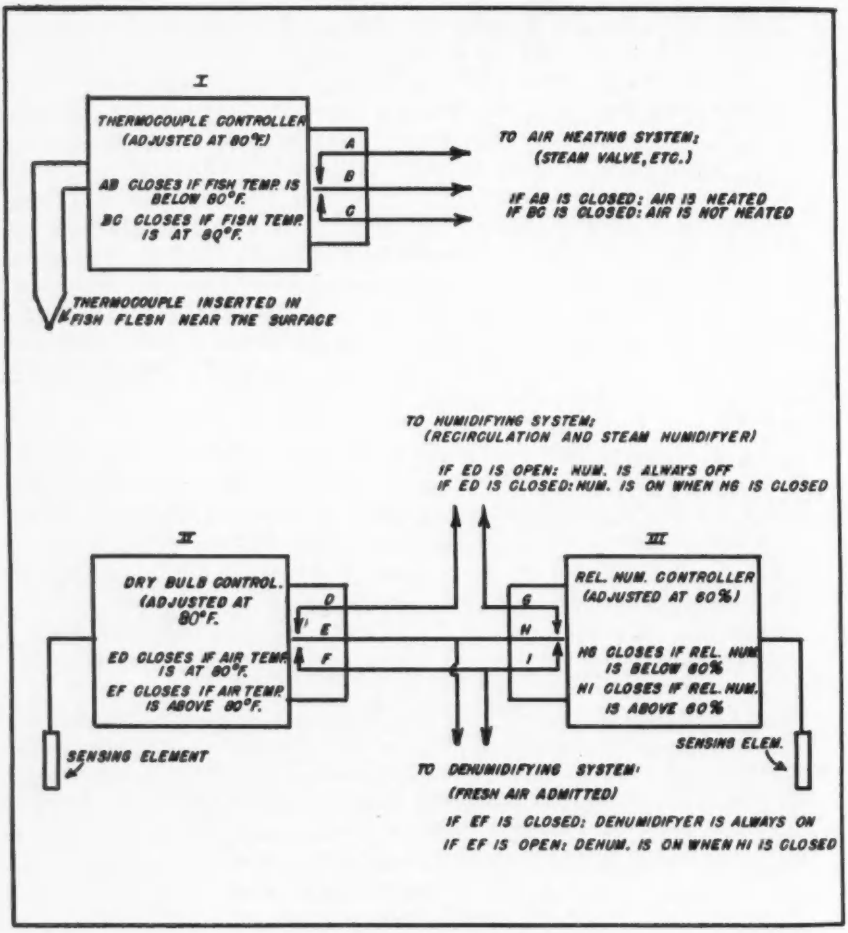

I
THERMOCOUPLE CONTROLLER (ADJUSTED AT 80°F.)
AB CLOSES IF FISH TEMP. IS BELOW 80°F.
BC CLOSES IF FISH TEMP. IS AT 80°F.
A
B
C
TO AIR HEATING SYSTEM: (STEAM VALVE, ETC.)
IF AB IS CLOSED: AIR IS HEATED
IF BC IS CLOSED: AIR IS NOT HEATED
THERMOCOUPLE INSERTED IN FISH FLESH NEAR THE SURFACE
TO HUMIDIFYING SYSTEM: (RECIRCULATION AND STEAM HUMIDIFYER)
IF ED IS OPEN: HUM. IS ALWAYS OFF
IF ED IS CLOSED: HUM. IS ON WHEN HG IS CLOSED
II
DRY BULB CONTROL. (ADJUSTED AT 80°F.
ED CLOSES IF AIR TEMP. IS AT 80°F.
EF CLOSES IF AIR TEMP. IS ABOVE 80°F.
D
E
F
III
REL. HUM. CONTROLLER (ADJUSTED AT 60%)
G
H
I
HG CLOSES IF REL. HUM. IS BELOW 60%
HI CLOSES IF REL. HUM. IS ABOVE 60%
SENSING ELEMENT
SENSING ELEM.
TO DEHUMIDIFYING SYSTEM: (FRESH AIR ADMITTED)
IF EF IS CLOSED: DEHUMIDIFYER IS ALWAYS ON
IF EF IS OPEN: DEHUM. IS ON WHEN HI IS CLOSED

FIG. 1. Thermocouple control system.

the surface gradually dries out and the cooling effect decreases correspondingly. Consequently, the temperature of the air is automatically and gradually lowered to 80°F. until the surface is completely dry. Controller systems II and III regulate the relative humidity. Dry-bulb temperature controller II and relative humidity controller III are adjusted to 80°F. and 60% respectively. As shown by the wiring diagram, the two controllers regulate the operation automatically and according to the conditions required at temperatures above and below 80°F. If the temperature of the air is higher than 80°F., as long as the surface of the product is still wet or partly wet, controller III shuts off and the relative humidity of the air is kept at the lowest possible level by the action of controller II. When the air temperature reaches 80°F. and when the surface of the product is completely dry, controller II stops dehumidifying and the relative humidity of the air is increased up to 60%, where it is maintained by controller III as long as the temperature does not exceed 80°F.

Instead of the relative humidity controller III a wet bulb controller could be installed, which would have to be adjusted to 69.5°F. (20.8°C.) in order to obtain a relative humidity of 60% when the air temperature is at 80°F. This would be cheaper, but the regulation thus obtained would not be ideal because the air temperature is indirectly controlled from the temperature of the fish and therefore is not constantly at 80°F. Consequently, some of the advantages of the process would be lost.

EXPERIMENTS

The trials were carried out in our experimental artificial dryer, which has a capacity of approximately 400 lb. (180 kg.). It is equipped with the thermocouple system of control described above. No external dehumidifier was used. However, when necessary, steam humidification was employed, in combination with recirculation of the air. A constant air velocity of 350 feet (110 m.) per minute was maintained throughout all experiments.

For each experiment the dryer was filled with fish of uniform, medium size which had been previously salted at this station using the conventional procedure for each particular product (heavy or light salted fish) investigated. Great care was taken in selecting fish of identical initial moisture content for all trials, because the drying rate is greatly influenced by this factor. The average moisture content of light salted fish was 75.6% wet basis or 310% dry basis, and of heavily salted fish 60% wet basis or 150% dry basis.

The loss in weight at each stage was followed on a torsion balance with five fish. All moisture content values refer to "dry basis" (pounds of water per 100 lb. of dry material) and the data recorded here represent the loss of moisture by the fish. This value, represented by the symbol L, is obtained by subtracting the actual moisture content (W) from the initial moisture content (W_0) at any given time (θ) during the drying operation. The drying rate $\frac{\Delta W}{\Delta \theta}$ may be obtained directly by a simple graphical differentiation of the moisture loss curve.

Isometric triaxial graphic representation (Fig. 2, 3 and 4) of the various drying curves has been used in order to obtain a maximum of information from a single Figure. On this type of graph each Figure presents three different curves so that the drying rate as well as moisture loss can be found for any moment of a drying experiment. The Figures show also the relation which exists between drying rate and moisture loss.

The moisture content of fish (dry basis) is easily calculated. As stated above, moisture loss L is the difference between initial (W_0) and actual (W) moisture content:

$$L = W_0 - W$$

and from our experiments we know that the initial moisture content

$W_0 = 310$ for light salted fish, and
$W_0 = 150$ for heavy salted fish.

Therefore, the moisture content W on dry basis is

$W = 310 - L$ for light salted fish, and
$W = 150 - L$ for heavy salted fish.

From W, the moisture content on wet basis can be calculated by the formula:

$$\text{Percentage water (wet basis)} = \frac{W}{W + 100} \times 100.$$

After drying, the final moisture content of salt fish will be:

$$W = 60 \text{ (for 37.5\% wet basis).}$$

Therefore, the total amount of water evaporated during drying was:

$W_0 - W_F = 310 - 60 = 250$ for light salted fish, and
$W_0 - W_F = 150 - 60 = 90$ for heavy salted fish.

Finally, the amount of water which has been evaporated at any point, expressed in percentage of the total amount which is to be removed, is calculated as follows:

$$\text{Percentage water evaporated} = \frac{L}{250} \times 100 \text{ for light salted fish, and}$$

$$= \frac{L}{90} \times 100 \text{ for heavy salted fish.}$$

Experiments were carried out using the ordinary as well as the thermocouple method of control in order to compare the results obtained with both methods. Drying runs were made with light salted fish of the Gaspé cure type and with heavily salted fish. With Gaspé cure fish, continuous as well as intermittent drying were investigated. Some experiments were also conducted under unfavourable atmospheric conditions when artificial drying would have been impossible with control methods generally used.

RESULTS AND DISCUSSIONS

Light Salted Fish—Gaspé Cure

(a) continuous drying

The drying curves obtained with continuously dried Gaspé cure fish are shown in Fig. 2. Curves I and II have been obtained with ordinary and thermocouple controls respectively. With ordinary control, the temperature of the drying air was maintained at 80°F., and the relative humidity at 55%. With thermocouple control, however, much higher temperatures and lower relative humidities were encountered as long as the fish surface was still moist. When atmospheric conditions were favourable, temperatures as high as 125°F. (52°C.) and relative humidities as low as 15 to 20% have been obtained. When the surface was completely dry, the air temperature was automatically lowered to 80°F. and the relative humidity was increased to 60%.

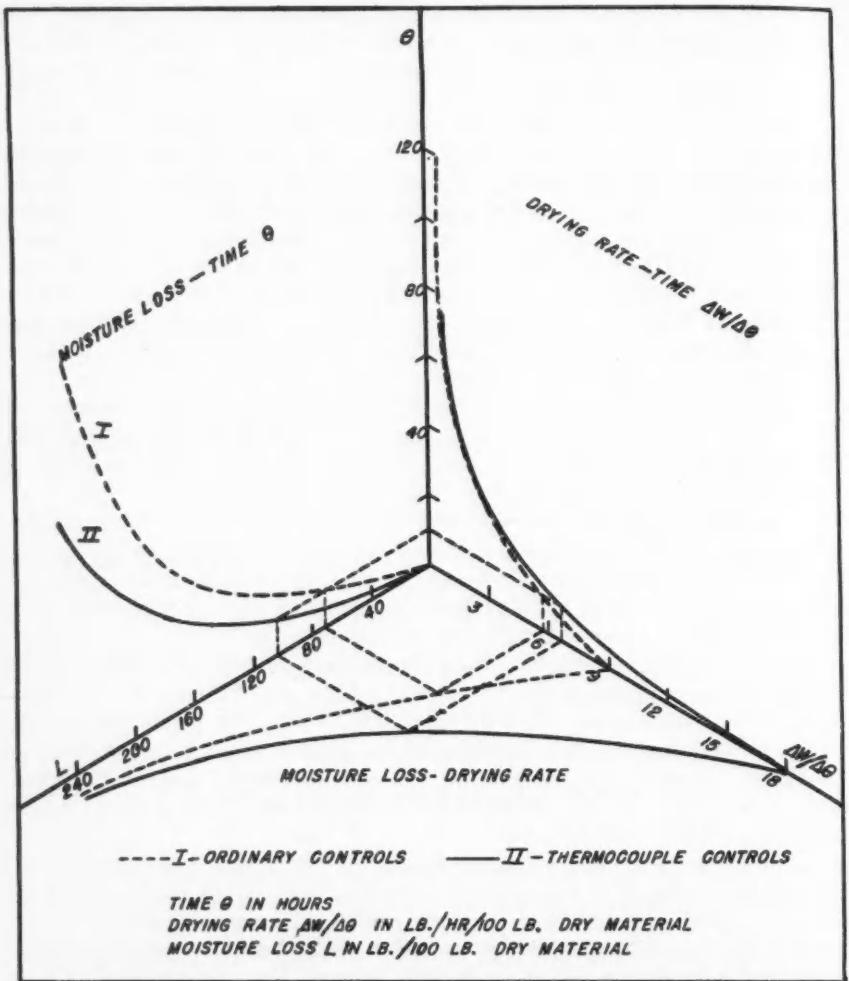
The moisture-loss curves show that 250 lb. water/100 lb. dry material have been removed after 120 hours of drying by the conventional method. With thermocouple control the same amount of water had already been removed at the end of 73½ hours.

The drying-rate curves show that by instrument control up to 18 lb. water/hour/100 lb. dry material are removed at the beginning of the drying operation. With ordinary control, the rate is only 9 lb. (4.1 kg.) water/hour. The difference in drying rates between the two methods of control decreases rapidly as long as water is removed from the fish surface. After about 20 hours of drying, the rates of the two methods are practically identical, namely 4.5 lb. water/hour/100 lb. dry material, and remain very similar till the end of the drying operation, because the surface of the fish is dry in both instances. This is only one quarter of the value observed at the beginning of the operation in the case of thermocouple control and about one half in the case of ordinary control. However, about 57% of the water has already been evaporated with thermocouple control and about 40% with ordinary control.

These experiments warrant the following conclusion: According to our present knowledge it is impossible to obtain a first quality product by continuous drying, although thermocouple control prevents overdrying of the surface. The formation of a thin layer of salt at the surface is a standard requirement in the appearance of light salt fish. This could not be attained without cross-piling. Therefore good Gaspé cure fish can be produced only by successive drying and cross-piling periods.

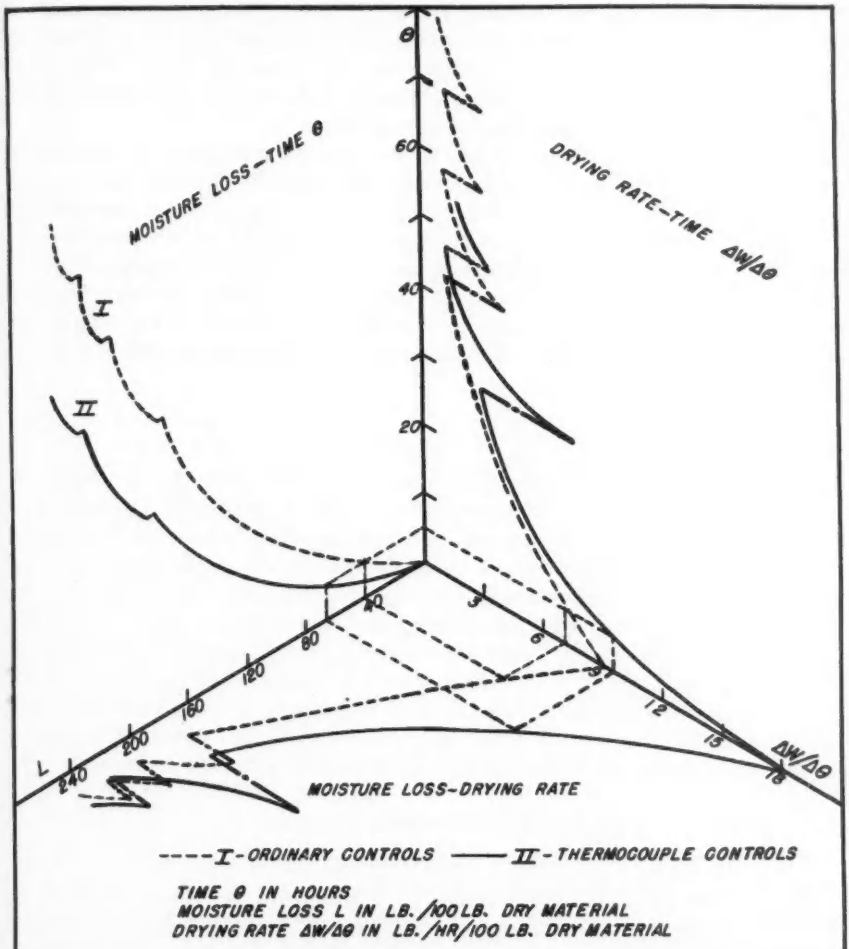
(b) multi-stage drying

In another series of experiments several successive drying periods were employed, cross-piling the salt fish during the intervals. The curves obtained are shown in Fig. 3. With ordinary control it was necessary to increase the relative humidity up to about 60% after the first drying period in order to obtain a first quality product. With thermocouple control however, the relative humidity is increased automatically as soon as the surface is dry.



FOR θ = 10 HOURS	THERMOCOUPLE CONTROLS	ORDINARY CONTROLS
DRYING RATE: ΔW/Δθ	6.7	5.6
MOISTURE LOSS: L	105	71
WATER CONTENT: W	310–105 = 205	310–71 = 239
% WATER (WET BASIS)	205/305 = 67.2	239/339 = 70.5
% OF WATER EVAPORATED	105/250 = 42.0	71/250 = 27.4

FIG. 2. Gaspé cured fish—continuous drying.



FOR θ = 5 HOURS	THERMOCOUPLE CONTROLS	ORDINARY CONTROLS
DRYING RATE: ΔW/Δθ	9.5	7.0
MOISTURE LOSS: L	68	40
WATER CONTENT: W	310−68 = 242	310−40=270
% WATER (WET BASIS)	242/342=70.8	270/370=73.0
% OF WATER EVAPORATED	68/250=27.2	40/250=16.0

FIG. 3. Gaspé cured fish—multi-stage drying.

As shown by the moisture-loss curves, 80 drying hours were required to remove 250 lb. moisture/100 lb. dry material with ordinary control, and 55 drying hours for the same proportion of moisture with thermocouple control. With intermittent drying, an increase in rate is obtained at the beginning of each period, because the cross-piled product has a wet surface.

In our experience, thermocouple control permits completion of the drying operation in three periods, which compares favourably with the four periods required with conventional control systems. This is because the new method results in the final moisture content of each period being lower than that obtained with the old method. Besides, it offers the advantage of saving time and labour for loading, unloading and cross-piling. Thermocouple control also minimizes the chances of over-drying the surface because this depends only on the adjustment of the controlling equipment. It is thus comparatively easy to obtain a choice quality product.

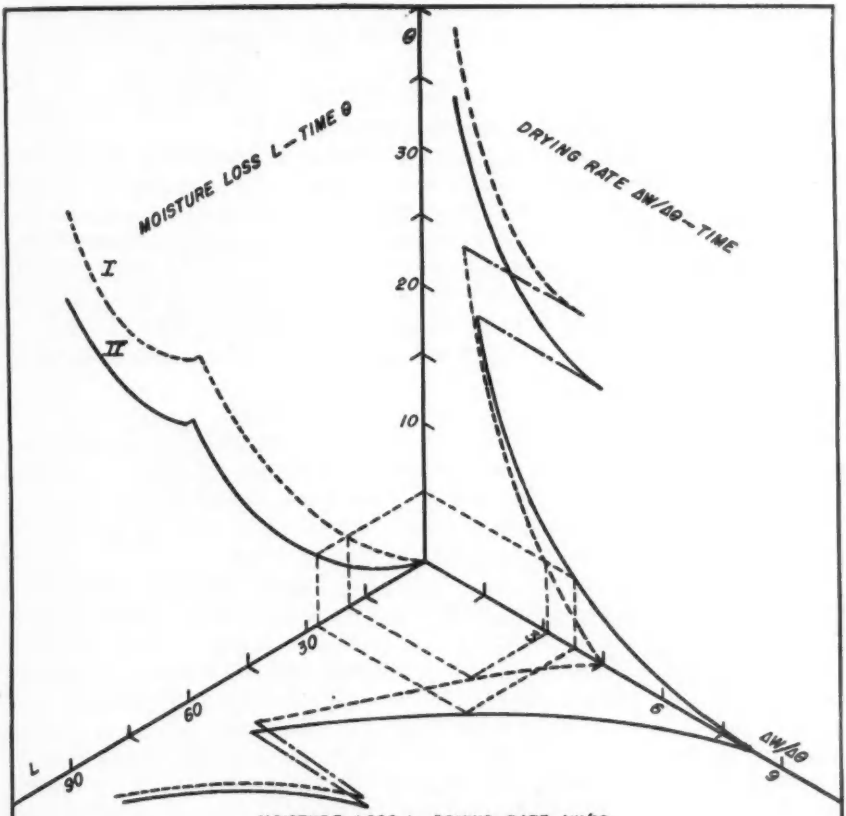
Heavy Salted Fish

The curves obtained from experiments with heavy salted fish are shown in Fig. 4. As with light salted fish, an increase in rate is obtained at the beginning of each period. The drying process was completed in 34 hours with thermocouple control as compared to 40 hours with ordinary control. With this product, the increase is not as great as with light salted fish because the initial moisture content is already much lower. A striking advantage of thermocouple control for the artificial drying of heavy salted fish consists in reducing the possibilities of formation of an impervious salt–protein crust on the fish surface. This crust is usually encountered when conditions giving high drying potentials are used with ordinary control. Therefore the use of thermocouple control renders it comparatively easy to obtain a product of good quality in spite of its high drying rate.

Atmospheric Conditions

In order to obtain acceptable, artificially dried salt fish with the conventional control system, the temperature inside the dryer should be maintained at 80°F. and the relative humidity at 55%. This is possible when the outside temperature is below 80°F. and the dew point below 55°F. (13°C.) (Legendre, 1953). Drying can still be carried out at dew points above 55°F. but at a slower rate so that, particularly at dew points between 60 and 65°F. (15.5 and 18.5°C.), light salted fish is subject to sliming. At dew points above 65°F., drying is impossible.

However the thermocouple system of control maintains in the dryer conditions which permit perfect operation at much higher dew points. As long as the surface of the fish is still wet, there are practically no limits as regards temperature, and good results can be obtained as long as the dew point does not exceed 72°F. (22°C.). When the surface is dry, the temperature must be below 80°F. and the dew point in the vicinity of 65°F. However, since there is no moisture at the surface, sliming is not encountered and drying is still possible, although at a reduced rate, with dew points up to 68°F. (20°C.).



FOR θ = 5 HOURS	THERMOCOUPLE CONTROLS	ORDINARY CONTROLS
DRYING RATE: ΔW/Δθ	3.75	3.1
MOISTURE LOSS: L	28	20
WATER CONTENT: W	150–28=122	150–20=130
% WATER (WET BASIS)	122/222=55.0	130/230=56.5
% OF WATER EVAPORATED	28/90=31.1	20/90=22.2

FIG. 4. Heavy salted fish.

Series of wet and dry bulb recordings have been made in six different fishing centres along the Gaspé Peninsula and it was found that the dew point never exceeded 67°F. (19.5°C.) (Legendre, 1952). During July and August, the dew point was in the vicinity of 65°F. for about 10%, between 55 and 65°F. for about 46%, and below 55°F. for about 44% of the time.

Consequently, artificial drying with ordinary control would, during this 2-month period, have been impossible on 6 days and quite hazardous on 27 days. With thermocouple control, however, satisfactory results would have been obtained on all 60 days. This has been confirmed by drying experiments made under unfavourable atmospheric conditions, that is to say, when artificial drying would have been impossible with ordinary control. The drying rates obtained with the new method and without an external dehumidifier were of the same order as with ordinary control if used under favourable atmospheric conditions.

SUMMARY

The thermocouple method of control proposed for artificial salt fish dryers permits constant and automatic regulation of temperature and relative humidity. It has the following advantages over the conventional method of control:

1. When atmospheric conditions are favourable for artificial drying, an increase in rate is obtained at the beginning of each drying period.

2. The system permits an increase in relative humidity as soon as the surface of the fish becomes dry, consequently the production of choice quality light or heavy salted fish is comparatively easy.

3. For light salted fish only three drying periods are required, compared with the four necessary by the conventional method. The possibilities of overdrying the surface or cooking are eliminated automatically.

4. Even under unfavourable atmospheric conditions, good results are obtained. External dehumidifiers are not required. The drying rate is comparable to that obtained with the old method under favourable atmospheric conditions.

The method is based on the general theory of drying and can therefore be used for the artificial drying of any other product, provided the highest temperature which the material tolerates and the lowest relative humidity which will give a product of good quality are known. The controls need only to be adjusted for these limits and ideal drying conditions will automatically be maintained at each instant of the operation.

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The Composition of the Fatty Acids Liberated from the Phospholipids in the Preparation of Salted Codfish[1]

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ABSTRACT

The component fatty acids of the phospholipids of fresh and light salted cod flesh were determined. During the preparation of light salted "Gaspé cure" codfish 77% of the phospholipidic fatty acids are set free. The fatty acids liberated are mainly the C_{20} and C_{22} highly unsaturated. The C_{22} acids have a mean unsaturation of −11.5 H. The C_{16} saturated and unsaturated acids are also preferentially liberated.

INTRODUCTION

It is known that free fatty acids are formed during the deterioration of fishery products. Stansby and Lemon (1941) noticed the formation of large quantities of fatty acids during spoilage of fresh mackerel. Hillig and Clark (1938) determined the increasing formation of volatile acids during the decomposition of canned salmon and tuna. Dyer and Morton (1956) followed in a few species of frozen fish the formation of free fatty acids paralleling the protein denaturation.

These investigators were preoccupied primarily with the formation of free fatty acids. Recently, however, Lovern (1956) published a thorough analysis of the total lipids of cod flesh, which showed that they consist of a complex mixture of different groups of lipids of which the phospholipids are the major components. In a preceding investigation on the changes occurring in the lipids of cod flesh during the preparation of salted fish, Cardin and Bordeleau (1957) found that a large decrease in the phospholipids content was accompanied by a proportional increase in free fatty acids and by an increase in the iodine value of the non-phospholipidic fraction of the lipids. It was suggested that the greater part of the fatty acids, liberated during salting, originated from the phospholipids which had been hydrolysed.

In the present investigation, the proportion as well as the character of unsaturation of the different fatty acids liberated from the phospholipids of cod flesh during the preparation of light salted codfish, were determined. To this effect, the component fatty acids of the phospholipids of cod flesh were determined before and after the preparation of saltfish, that is in fresh fish and in light salted "Gaspé cure".

MATERIALS AND METHODS

Gaspé cure light salted codfish was prepared by adding 8 lb. of salt per 100 lb. of split fish. The fish was kept 48 hours in the salt then dried in three stages to 38% moisture content.

[1]Received for publication December 12, 1957.

J. Fish. Res. Bd. Canada, 15(4), pp. 555–558, 1958.
Printed in Canada.

Hundred-gram portions of both the fresh and cured fish were extracted successively with 200-ml. portions of acetone, ethyl alcohol, and petroleum ether of b.p. 40 to 60°C. under reflux for 4 hours. The acetone and alcohol extracts were freed from solvents and the aqueous residues obtained were re-extracted with petroleum ether. The lipid extract is estimated to be representative of the total lipids present in the flesh and has been verified (Folch *et al.*, 1951) to be free from contaminating non-lipid material.

The phospholipids were separated from the total lipid extract through three successive precipitations from a solution in ether by 10 volumes (wt./vol.) of acetone at 0°C. overnight.

The phospholipids were hydrolyzed by refluxing with 1% H_2SO_4 in ethanol for 3 hours (Hawke, 1955) and then with 7% KOH in ethanol for a maximum of 2 hours to prevent possible re-arrangement of the highly unsaturated acids. The mixture was acidified and the mixed fatty acids obtained were fractionated by successive crystallization in 10 volumes (wt./vol.) of acetone or ethyl ether at low temperatures (Table I).

TABLE I. Low-temperature crystallization of the phospholipid fatty acids in fresh and Gaspé cure cod flesh.

Fraction	Description		Weight	Weight	Iodine value
			g.	%	
Fresh fish	Mixed fatty acids				240.6
A	Insoluble in ether at	−40°C.	8.7	26.1	23.9
B	Soluble in ether at	−40°C.	5.2	15.7	103.6
C	Soluble in acetone at	−75°C.	19.4	58.2	363.7
Gaspé cure	Mixed fatty acids				206.6
A	Insoluble in acetone at	−40°C.	5.3	31.1	23.1
B	Soluble in acetone at	−40°C.	3.4	19.9	130.9
C	Soluble in acetone at	−70°C.	8.3	49.0	356.3

The fractions obtained were converted into methyl esters which were fractionally distilled in the usual way. The composition of each ester fraction obtained was calculated from its saponification equivalent and iodine value (Hilditch, 1947) and the component fatty acids so derived are listed in Table II.

The saponification equivalent was determined on 0.2 g. of methyl esters using absolute ethyl alcohol, and titrating with alcoholic HCl under a constant atmosphere of CO_2-free nitrogen (Desnuelle and Constantin, 1952).

RESULTS AND DISCUSSION

The few available analyses of the component fatty acids of the phospholipids of fish tissues show basic differences which are not present in the triglycerides of fish depot fats. In fact, highly unsaturated C_{20} and C_{22} fatty acids are reported to be absent in purified lecithin from salmon eggs (Anno, 1949). Purified lecithin from shark eggs has no hexadecenoic acid, a low proportion of C_{20} and C_{22} polyethylenic acids and a high (35%) proportion of palmitic acid (Igaraschi *et al.*, 1955). On the other hand, the fatty acid composition of cod flesh phospholipids given in Table II is similar to that of haddock flesh phospholipids (Lovern, 1956) except for the absence of C_{16} unsaturated acids in the latter. The phospholipids

of cod flesh also have the same general composition as total phospholipid preparations from the roe of the New Zealand ling (Shorland, 1939) and from the liver of the groper (Shorland and Hilditch, 1938), which contain a higher proportion of C_{20} and C_{22} unsaturated acids and of stearic acid than is usually found in the triglycerides of fish depot fats.

TABLE II. Component fatty acids of phospholipids excluding unsaponifiable.

Acids	From fresh cod flesh		From Gaspé cure cod flesh	
	% wt. (g.)		% wt. (g.)	
Saturated				
C_{14}	0.13		...	
C_{16}	14.95		9.21	
C_{18}	8.47		16.02	
C_{20}	0.98		4.33	
Unsaturated				
C_{16}	4.58	(- 2.1 H)*	0.85	(- 2.0 H)
C_{18}	13.38	(- 2.5 H)	12.73	(- 2.9 H)
C_{20}	21.90	(- 7.1 H)	28.05	(- 4.8 H)
C_{22}	34.91	(-11.4 H)	28.81	(-11.0 H)
C_{24}	0.70	(-11.8 H)	...	

*Mean unsaturation in parentheses, as deficiency of hydrogen atoms.

Fresh cod flesh was found to contain 3.2% of total lipids (dry basis), 67.7% of which are phospholipids containing 68% of fatty acids. Gaspé cure cod flesh contained 3.5% total lipids (dry basis, excluding salt), 17.2% of these lipids being phospholipids containing 57.7% of fatty acids. Consequently, one kilogram of dry material (excluding salt) from fresh and Gaspé cure cod flesh contains 15.0 g. and 3.5 g. respectively of phospholipidic fatty acids. Therefore, 77% by weight of the phospholipidic fatty acids was liberated during the preparation of Gaspé cure codfish.

Knowing from Table II the component fatty acids (% wt.) before and after salting, the proportion as well as the mean unsaturation of each group of fatty acids liberated during salting have been calculated.

TABLE III. Fatty acids liberated from the phospholipids during preparation of light salted codfish.

Acids	Fresh fish		Light salted fish		Acids liberated	
	% wt. (g.)		% wt. (g.)		% wt. (g.)	
Saturated						
C_{14}	0.1		...		0.1	
C_{16}	14.9		2.2		12.7	
C_{18}	8.5		3.7		4.8	
C_{20}	1.0		1.0		0.0	
Unsaturated						
C_{16}	4.6	(- 2.1 H)*	0.2	(- 2.0 H)	4.4	(- 2.1 H)
C_{18}	13.4	(- 2.5 H)	3.0	(- 2.9 H)	10.4	(- 2.4 H)
C_{20}	21.9	(- 7.1 H)	6.5	(- 4.8 H)	15.4	(- 8.1 H)
C_{22}	34.9	(-11.4 H)	6.7	(-11.0 H)	28.2	(-11.5 H)
C_{24}	0.7	(-11.8 H)	...		0.7	(-11.8 H)
Total	100.0		23.3		76.7	

*Mean unsaturation in parentheses, as deficiency of hydrogen atoms.

Of the major component phospholipid fatty acids of fresh cod flesh, the C_{16}, both saturated and unsaturated, are the acids which are liberated in the largest proportion during salting (Table III). The C_{18}, C_{20} and C_{22} unsaturated acids are set free in about equal proportions. However, since the C_{20} and C_{22} unsaturated acids are present in large quantities in the phospholipidic acids of fresh cod flesh, these two groups of acids make up 57% of all the fatty acids liberated during salting.

The mean unsaturation of the C_{20} and C_{22} acids in the phospholipids is lower in salted fish than in fresh fish, indicating that the most highly unsaturated acids of these two groups of acids are liberated during salting. Since the mean unsaturation of the C_{22} unsaturated acids is –11.4 H and –11.0 H before and after salting, it can be calculated that the C_{22} acids liberated during salting are of a mean unsaturation of approximately –11.5 H. This small decrease in mean unsaturation of the C_{22} acids during salting may be also the result of a slight oxidation.

Although about 23% of the acids liberated are saturated acids, the great proportion and the very high unsaturation of the C_{20} and C_{22} acids give an approximate calculated iodine value of 239.6 for the total fatty acids liberated.

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Toleration of Fish to Toxic Pollution[1,2]

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INTRODUCTION

This paper reviews the results of research on toleration of fish to toxic pollution made known since the critical review of the literature on the subject by Doudoroff and Katz (5). The purpose is to bring together the work being carried out in the United Kingdom, the United States and Canada in this field. It is restricted to three aspects of the subject:

1. The relationship between concentration of toxic material and survival time;
2. The effect of factors other than concentration of toxic material on survival time in a toxic solution;
3. Toleration in the wider sense of ability of the species to prosper in the environment as opposed to mere ability of the individual to survive.

RELATIONSHIP BETWEEN CONCENTRATION OF TOXIC MATERIAL AND SURVIVAL TIME

In 1952 Herbert and Merkens (10, 11) published the results of their studies on the survival of rainbow trout in solutions of potassium cyanide. The results are of particular interest because they were exhaustive and also because the construction of a special apparatus made possible very close control of environmental conditions with a constant flow of toxic solution.

The authors discuss different methods of expressing their results. Figure 1 shows the type of curve obtained if their data are plotted according to the method proposed by Powers (16), except that the reciprocal of median survival time (as defined below) is used instead of the reciprocal of individual survival times. The resulting curve is similar to that obtained by Powers using goldfish as the test fish. In accordance with Powers practice the dotted straight line has been fitted to the central part of the curve where the slope is steepest. If produced to the horizontal axis it cuts it at a point corresponding with a concentration of 0.14 ppm of cyanide. If the straight line relationship held throughout the range of concentrations this would be the lower threshold concentration. The experimental results show that there is a measurable toxicity at a concentration of 0.14 ppm of cyanide. These results illustrate the danger of measuring survival time only at concentrations in the range corresponding with the straight line part of the curve and extrapolating beyond the range in which the relationship holds.

The authors tested their data both by plotting probits corresponding to percentages of fish overturned against survival time, log survival time and reciprocal survival time and also by examining goodness of fit mathematically. Both methods

[1]Received for publication February 28, 1958.

[2]A paper presented at the 11th Meeting of the Canadian Committee on Freshwater Fisheries Research, at Ottawa, January 3, 1958.

J. Fish. Res. Bd. Canada, 15(4), pp. 559–572, 1958.
Printed in Canada.

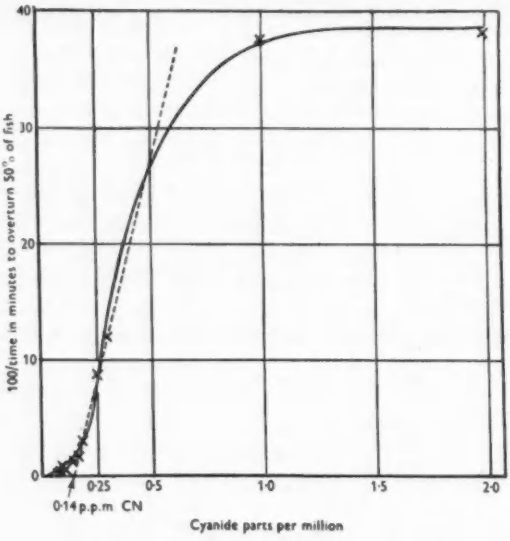

FIG. 1. Relation between concentration of cyanide and reaction time of fish plotted according to method of Powers (1917). (From Herbert and Merkens, 1952, p. 646.)

show that the log transformation is markedly superior to the other two forms for their data.

Figure 2 shows median survival times plotted against concentration of cyanide in parts per million, both in log scales. The "median" survival time as used by Herbert and Merkens, and in this paper, is not the usual statistical median, but is the geometric mean of survival times at each concentration, given by the formula:

$$\text{M.S.T.} = \text{antilog}\left(\frac{\Sigma \log T}{N}\right)$$

where T is the survival time of each fish and N is the number of fish in the test.

The straight line portion of Figure 2 can be represented by the equation:

$$C^n T = K$$

where C is concentration in ppm, T is the median survival time, and n and K are constants. This same formula has been applied by Ostwald (15) to data obtained by studying the survival of *Gammarus* in different dilutions of sea water, and Chick (4) found that it held for the relationship between concentration of several disinfectants and time taken to kill bacteria.

The dotted line on either side of AA′ in Figure 2 shows the 95% confidence limits for points corresponding with concentrations of less than 0.2 ppm cyanide. All points below 0.2 ppm lie within these limits. Between 0.25 and 0.3 ppm cyanide the data departs from the straight line relationship.

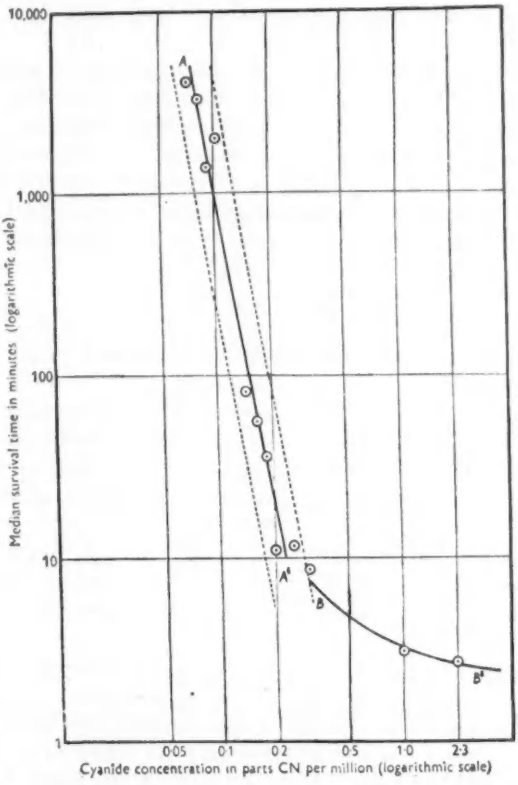

FIG. 2. Relation between concentration of cyanide and survival time of rainbow trout at 17.5°C. The points represent the median survival times and the dotted lines 95% confidence limits calculated from the scatter of the seven longest median survival times about the fitted lines A–A′ and B–B′. (From Herbert and Merkens, 1952, p. 643.)

Herbert and Merkens' data extend only to medium survival times up to 4,441 minutes but in (10) the authors calculate that at a concentration of 0.023 ppm cyanide the median survival time would be 5 years. They point out that before this time had elapsed many factors besides toxicity would have affected mortality.

Alderdice and Brett (1) have published the results of their studies on the toxicity of kraft pulp mill wastes to young sockeye salmon. In this case not only were the medium (sea water) and the species of fish different, but the toxic material, instead of being a pure substance, was a complex mixture of imperfectly known composition. The experimental method differed in detail from that used

by Herbert and Merkens, but it is doubtful if these differences invalidate comparison of the results.

In this paper the authors set out in detail the methods by which they analysed their results. Unlike Herbert and Merkens they found that with their data there was a slight advantage statistically in using the reciprocal rather than the logarithmic series. Figure 3a shows the probit response log mortality-time curves for concentrations from 5% to 18% effluent. These can be compared with the centre curve of Figure 3b which is from Herbert and Merkens' data for 0.14 ppm cyanide.

Alderdice and Brett derived a special hyperbola equivalent to the straight line

$$u = \alpha + \beta v$$

where u equals the reciprocal of mean survival times and v equals the reciprocal of effluent concentrations.

The asymptote $-\beta/\alpha$ provides an estimate of the concentration of effluent which is safe in terms of the experimental fish for all durations of exposure. Using the experimental data they obtained an estimate of the value of $-\beta/\alpha$ with confidence limits for the true value and found them to be 4.8% of effluent with 95% limits of 4% and 5.4%.

In Figure 3a the dotted extension of the 5% line indicates a possibility that this line is truncated. This led the authors to suspect that a 4.8% line might consist of one or two points with a slope approaching zero (private communication).

Burdick (3) has proposed a method of treatment of toxicity data from which the threshold value for toxicity can be directly obtained. He has set up the hypothesis that the curvature of plots of concentration against survival time on log paper is due to failure of the effective range to conform to the axes of the paper. This is because there is a minimum time to death, which is controlled by the time taken for the poison to enter the system of the fish and react, and a minimum concentration—the threshold value—beyond which survival time is independent of concentration. If minimum survival time is subtracted from time to death and the minimum concentration from the corresponding figure for concentration throughout the data, then the plot becomes a straight line.

The author found it difficult to measure the minimum time to death and minimum concentration from the experimental data. They can, however, be obtained from the graph. At low concentrations the time correction is insignificant on a logarithmic plot. If, therefore, different small values are subtracted from the concentrations over the lower range one value for the subtractions will give a straight line plot. This value is assumed to be the threshold concentration. If the same value is subtracted over the whole range of concentrations there will be a curvature at the end of the line corresponding to higher concentrations. This is due to the minimum survival time being significant at higher concentrations. The amount that must be deducted from the time co-ordinates to straighten this end of the line is a measure of the minimum time for death.

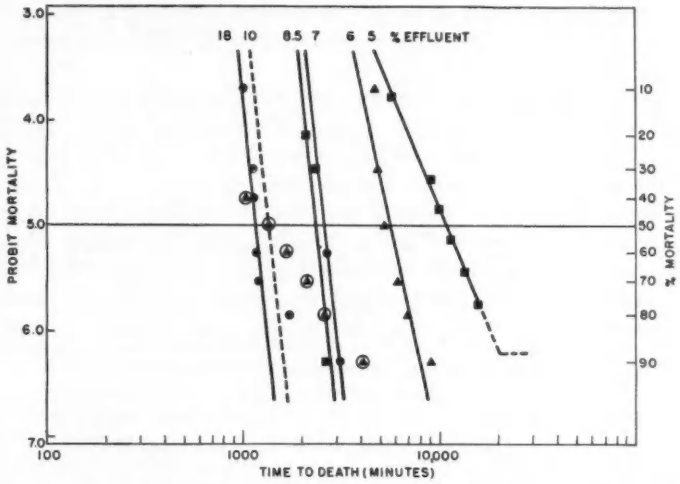

FIG. 3a. Time–mortality curves for sockeye salmon underyearlings exposed to various concentrations of kraft mill effluent. The figures in the graph represent percentage effluent in the several dilutions. (From Alderdice and Brett, 1957, p. 783.)

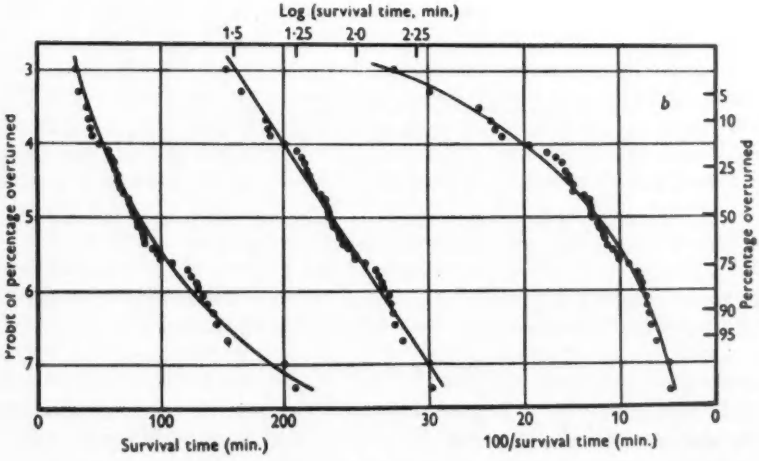

FIG. 3b. Survival times of rainbow trout in a solution containing 0.14 parts CN per million at 17.5°C. Probits corresponding to percentage survivors plotted against time, log time, and rate. (From Herbert and Merkens, 1952, p. 640.)

Burdick points out that although the method has been applied to several toxicity curves, final confirmation must await testing by application to many more sets of experimental data.

Herbert, Elkins, Mann and Hemens (12) give the results of their work on the toxicity of a mixture of household detergents to rainbow trout. The chemical composition of the mixture was not known, but it was selected as representative of the mixture likely to occur in an average sewer.

The authors found the "median" period of survival fell from 12 weeks at 3 ppm of surface active agent to half a day at 12 ppm. The surface active agent was expressed as Manoxol O.T. determined by the methylene blue method as recommended by Longwell and Maniece. The values for these and intermediate concentrations, as shown in Figure 4, when plotted as logarithms of concentrations

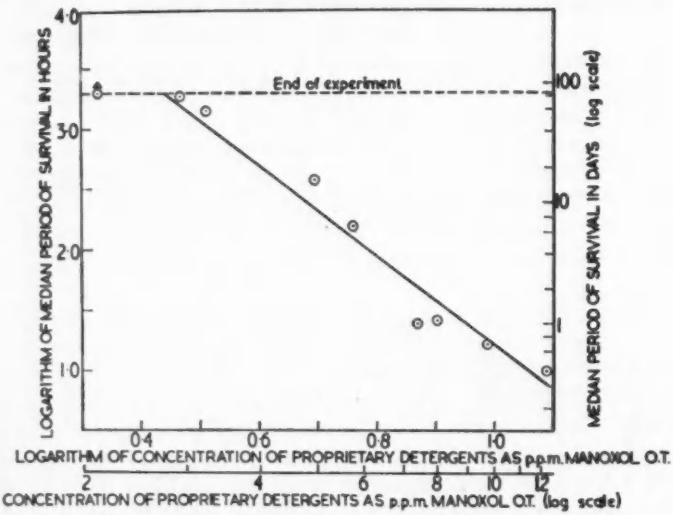

FIG. 4. Toxicity of a mixture of proprietary synthetic detergents to rainbow trout at 17.5°C. (From Herbert *et al.*, 1957.)

of detergents against logarithms of median survival times approximated to a straight line, which was reasonably well fitted by the equation:

$$\log T = K - n \log C$$

where T equals median (i.e. geometric mean) period of survival in hours, C equals concentration of active material as ppm Manoxol O.T., K equals 4.93, and n equals 3.71.

In this case the authors did not attempt to calculate a threshold value of safe concentration from the data. It was found that if the detergents were mixed with domestic sewage and passed through either a percolating biological filter or an activated sludge plant their toxicity was greatly reduced—see Figure 5. As most

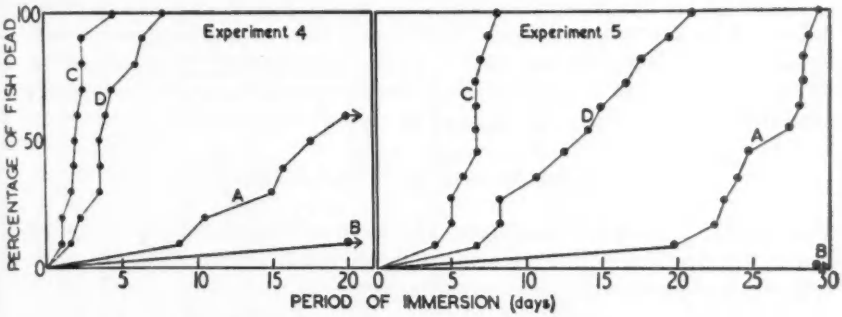

FIG. 5. Effect of biological filtration on toxicity of synthetic detergents.
A. Effluent from percolating filters treating sewage containing mixed detergents.
B. Effluent from percolating filters treating sewage containing no detergents.
C. Water plus mixed detergents.
D. Water plus sodium tetrapropylene benzene sulphonate.
Average concentration of surface active material in A was 9.2 ppm as Manoxol O.T. in Expt. 4, 9.6 ppm in Expt. 5. (From Herbert *et al.*, 1957.)

sewage in Britain is treated by one of these methods before disposal to a river and concentrations above 3 ppm are seldom found, it was concluded that there was unlikely to be toxicity due to the presence of detergents in domestic sewage in British rivers.

Many of the United States workers in this field in recent years have adopted a different approach to the problem from those already described. Doudoroff *et al.* (6) suggested a bioassay method of evaluating toxicity which has since formed the basis of much of the work in this field in the United States.

The method consists of measuring the toxicity of a number of different concentrations of poisonous material in the range of concentrations which give an appreciable number of deaths in 24, 48, and 96 hours. From this data a median tolerance limit (TI_m) is calculated. This is the concentration which will kill 50% of the test fish in 24, 48, or 96 hours under the conditions of the test.

This method, although a valuable measure of toxicity, does not allow estimates to be readily made of the concentration of the substance which will not be toxic in a measurable period. Some workers have suggested an application factor of $0.1 \times TL_m$ as a working compromise, but so far this is little more than an intelligent guess. However, in practice the TL_m is sometimes the only measure of toxicity that is available and as such it is valuable, providing its shortcomings are recognized.

Recently Henderson and Tarzwell (9) have used TL_m measurements in a practical application of considerable importance, which does not suffer from the shortcomings mentioned above. They found that where there were several sources of toxicity in a mixed effluent, the TL_m values of the component parts were additive in the total TL_m. By calculating the TL_m values for each component, it was therefore possible to measure the contribution of each to the total toxicity.

This method can be used both to assess the contribution of each of a number of different toxic effluents to the total toxicity of a body of receiving water and to assess the contribution of each process to the toxicity of the total effluent in a single industrial plant. For convenience of comparison Dilution Volume is calculated from the TL_m values. This is given by the following formula:

$$\text{Dilution Volume} = \frac{100 - TL_m}{TL_m} \times \text{Effluent Flow}$$

Dilution Volume is the dilution water needed to reduce the toxicity of the total flow to 50% mortality of test fish and can be expressed as cubic feet per second, million gallons per day, or gallons per minute.

THE EFFECT OF FACTORS OTHER THAN CONCENTRATION OF TOXIC MATERIAL ON SURVIVAL TIME

Many factors beside concentration of toxic material affect toleration by fish of toxic pollution. Among those which have been investigated are individual differences between fish, period of acclimatization, dissolved oxygen concentration, temperature, pH, and carbon dioxide concentration. Only the first three are considered here, although others are, in certain circumstances, of equal importance.

Herbert and Merkens (10, 11) examined the individual variation of fish to toleration of cyanide in considerable detail. They carried out toxicity tests on a fairly large number of fish, of as nearly as possible identical history and characteristics, at different concentrations of cyanide. The results for 0.14 ppm cyanide are illustrated in Figure 6. Figure 6a shows the result obtained by plotting percentage survival against time in minutes. Figure 6b shows the same data plotted as a frequency distribution with numbers of fish overturning in successive equal intervals of time. Figure 6c is the same except that log time is used instead of time as abscissa. Figure 6d shows a normal frequency curve. It will be seen that when time is used as abscissa there is a very pronounced tail to the curve. If log time is used, although the curve is still asymmetrical, it approximates more closely to the normal curve.

These authors carried out a detailed statistical analysis of their data and found that for cyanide the log transformation was markedly superior to either survival time or reciprocal of survival time. From this it follows that the best statistic for practical use to estimate the reaction of a sample to toxicity is the geometric mean or so-called median survival time as defined on page 560.

As briefly mentioned earlier, Alderdice and Brett (1) subjected their data to statistical analysis and found that calculation of the correlation coefficients for a measure of association between mean and standard deviation in the reciprocal and logarithmic series yielded values of $P \simeq 0.90, 0.85$ respectively, indicating a slight advantage in using the reciprocal. This raises the question of whether or not there is a difference in the mechanism of toxicity of a solution of a simple substance like cyanide and a complex solution such as pulp mill effluent.

Herbert and Merkens found that if fish were removed from the cyanide solution before they died and placed in clean water to recover and were later

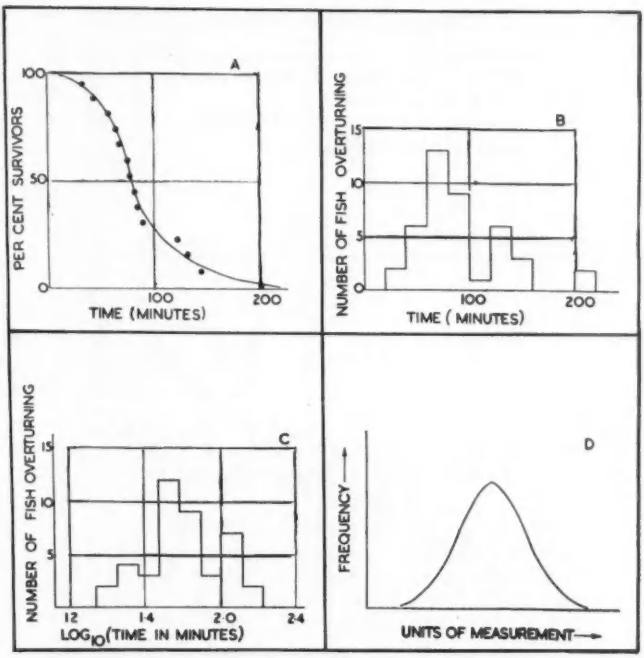

FIG. 6. Distribution of survival times of rainbow trout in 0.14 parts of cyanide per million at 17.5°C.

A. Percentage survivors plotted against survival time (points for every third fish only are shown).
B. The number of fish overturning in successive equal intervals of the logarithms of time.
C. The number of fish overturning in successive equal intervals of time.
D. A normal distribution curve.

(From Herbert, 1952.)

subjected to further tests, the individuals which survived longest in the first test also survived longest in the subsequent test. This indicates that resistance is an inherent quality in the individual fish.

Kathleen Downing (7) has investigated the effect of dissolved oxygen concentration on the toxicity of potassium cyanide to rainbow trout. In 27 tests she measured the period of survival of the fish in 3 different concentrations of cyanide and in 9 different concentrations of dissolved oxygen at each cyanide concentration. Her results are summarized in Figure 7.

First, it is clear that at each concentration the survival time increases with increase in concentration of dissolved oxygen. The increase is more noticeable in higher concentrations of dissolved oxygen than in lower concentrations (slope of curves increases). It was also more noticeable for lower than higher concentrations of cyanide.

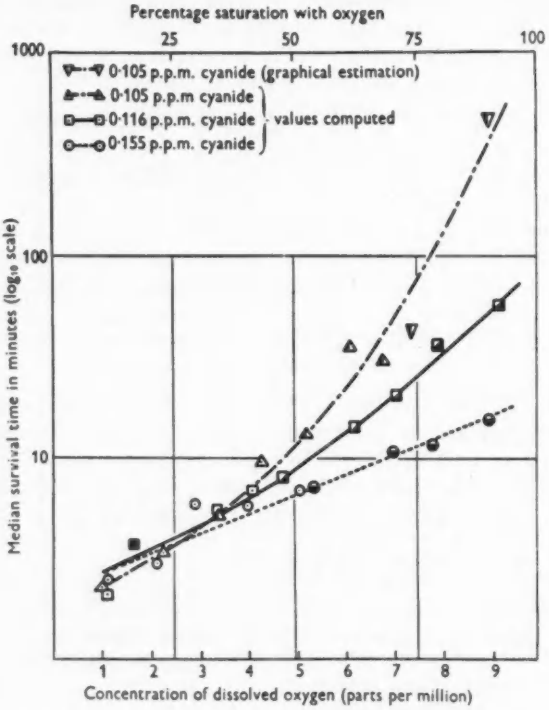

FIG. 7. Effect of concentration of oxygen on the period of survival of rainbow trout in solutions of potassium cyanide. The half-shaded points are those in which the distribution of survival time is log normal; distributions for other points are normal; the shaded point is that in which survival time appears to fit both a normal and log normal distribution. (From Downing, 1954, p. 163.)

Herbert, Elkins and Mann (12) measured the effect of dissolved oxygen on the survival time of rainbow trout in synthetic detergents. They found that an increase in dissolved oxygen from 4 to 8 parts per million doubled the median periods of survival time. Figure 8 shows the curve fitted by eye to their results.

Alderdice and Brett considered the relationship between the onset of respiratory distress, as indicated by gasping, and effluent concentration. They found, admittedly on limited data, that there was a tendency for respiratory distress to be observed at higher dissolved oxygen concentrations in higher than in lower effluent concentrations.

By relating these observations to available oxygen at different effluent concentrations they estimated that the safe concentration of effluent considering both the onset of respiratory difficulty and toxicity would be 2.5% instead of 4.8% considering effluent alone. Figure 9 shows their estimate of the availability of oxygen and estimated oxygen requirement for respiration.

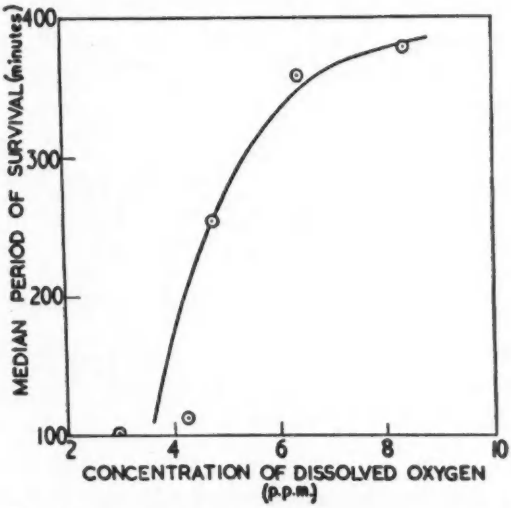

FIG. 8. Effect of dissolved oxygen concentration on the period of survival of rainbow trout in a solution of mixed proprietary synthetic detergents containing surface active material equivalent to 12 ppm Manoxol O.T.; temperature 18.5°C. (From Herbert *et al.*, 1957.)

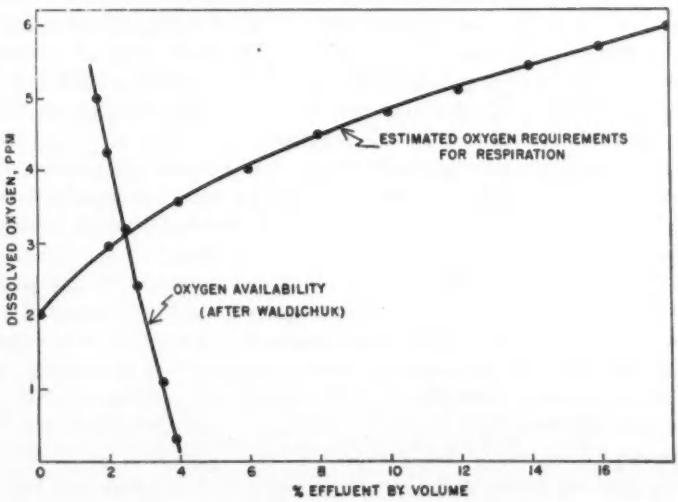

FIG. 9. Comparison of calculated net oxygen availability after effluent oxidation with respiratory requirements of sockeye salmon underyearlings at various concentrations of kraft mill effluent. The point of intersection of the curves, equivalent to a concentration of 2.5% effluent in the receiving water, provides an estimate of the concentration of effluent at which oxygen availability becomes a limiting factor for fishes in terms of the test conditions. (From Alderdice and Brett, 1957, p. 793.)

Weiss and Botts (18) have reported the results of experiments to test the effect of different dissolved oxygen concentrations on both survival time and oxygen consumption in solutions of Sarin. Their results correspond generally with those of Downing for cyanide.

Herbert and Merkens (11) carried out a series of tests of the effect of period of acclimatization of the test fish to test conditions on their survival time in 0.15 ppm of cyanide. They found there was a statistically significant difference in survival time in acclimatization periods from 24 to 191 hours. They did not continue the experiment sufficiently long to discover whether a steady state was eventually reached, but showed that if so, it would exceed 8 days. This demonstrates the necessity of standardizing acclimatization time in laboratory toxicity tests.

Weiss and Botts (18) found that the time to 50% mortality (T_{50}) for sunfish, minnows and goldfish increased with increased length of acclimatization in the laboratory prior to carrying out the tests.

THE WIDER ASPECTS OF TOLERATION OF TOXICITY

So far, only laboratory measurements of toleration of toxicity have been considered. At best these measure only the degree of intolerance of the fish to toxic substances under the test conditions. For practical purposes these results have to be related to the wider test of whether the fish can prosper as a species in an environment containing toxic pollution. To answer this question it is necessary to look, not merely at the ability of the individual fish to survive, but also its ability to compete with other fish and with physical factors of the environment, such as current, its ability to obtain and utilize food, and of suitable food organisms to survive. Reproduction, including the possibility of obtaining access to difficult spawning sites, and the ability of the eggs and young stages to develop normally, must also be taken into consideration.

To obtain answers to all these questions is even more difficult than obtaining satisfactory results from laboratory tests. Field tests must be carried out and these are frequently less exact in their methodology and more difficult to interpret than laboratory tests.

Allan, Alabaster and Herbert (2) have reported the results of a preliminary field test of this kind. They retained fish in cages in the effluent stream of a sewage works and also trapped fish living in the stream. In this case the only known toxic substances present were ammonia and carbon dioxide. It is interesting that they report that the effluent channel as a whole supported a large and varied population of coarse fish, although chemical conditions were sometimes found which, from laboratory tests, would not be expected to be capable of supporting fish.

I have kept fish in boxes in rivers in the past two years and have found them to survive for several weeks in situations in which there was marked pollution as measured by both chemical sampling and biological surveys.

Jones, Warren, Bond and Doudoroff (13) have carried out tests on the avoidance reactions of Pacific salmon to pulp mill effluent. Chinook salmon showed marked avoidance of toxic concentrations of sulphate and sulphite wastes.

Coho salmon showed considerably reduced avoidance reactions compared to the chinook salmon.

Neil (14) has measured the effect of sublethal concentrations of cyanide (0.01, 0.03 and 0.05 ppm) on the ability of speckled trout to perform work by swimming in a circular chamber revolving at 45 rpm. He found that although there was no measurable toxicity at these concentrations the ability of the fish to perform work was reduced by 75%, 90% and 98% respectively.

Warren and Doudoroff (17) have described an extensive programme of tests at present being undertaken at Oregon State College, Cornwallis, to investigate the long-term effects of pulp mill wastes on fish and the organisms on which they depend. These include tests in artificial streams and in small natural streams artificially contaminated with controlled amounts of pulp mill wastes. Results of these experiments are not yet available, but when they are they should go a considerable way towards an understanding of the wider aspects of toleration of toxicity and possibly of methods of deriving a relationship between toxicity as measured in laboratory tests and toleration of toxicity in the natural habitat.

CONCLUSIONS

The field biologist who is faced with the problem of determining whether a particular toxic pollution will be harmful to a fishery suffers from a severe lack of reliable data. Certain tests, such as TL_m estimations, or those of Herbert or Alderdice and Brett, are available, but these will not give him a complete answer. There remains a whole group of unknown, or but partly known, sub-lethal stresses for which he has no means of direct measurement.

Current research is moving towards reduction of the unknown factors in this field, but there is still much to be done. In the meantime the best he can do is use the existing methods to obtain the best available estimates and test these estimates by means of biological surveys carried out in the field. Ultimately the test of whether a fish tolerates a particular toxic pollution is whether it continues to prosper in an environment in which it previously prospered and into which the pollution has been introduced. The work of the past seven years has, however, enabled him to make better estimates of the likelihood of it prospering than was formerly possible.

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Hyperactivity as a Lethal Factor in Fish[1,2]

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ABSTRACT

Death occurs in fishes under certain circumstances following severe muscular activity. The precise cause of death is not yet known. However, it is possible that the severe disturbance to acid-base relationships following the large increase of lactic acid liberated from muscle glycogen may be the principal cause of death. Hyperactivity as a lethal factor in fishes is important in the study of biology of fishes and fisheries management.

INTRODUCTION

Von Buddenbrock (1938) was the first to appreciate that severe muscular exertion in fishes could result in their death. His observations have been amply substantiated by other workers (see Table I).

The degree of muscular exertion must not only have been severe but must also have been sustained in order to cause death; that is to say a fish will probably not die because of a single spurt of strenuous activity. The degree of activity would appear to be similar to the fastest rate of running for man, such as in a sprint. It will be noted that in all instances the exercise induced was brought about by man-made contrivances.

Some mention should also be made of the question of activity of fishes before going on to a detailed discussion. For this paper, three degrees of activity will be recognized, namely, no activity or the merest approach to it which is often referred to as the unexercised condition; moderate activity which would approximate cruising speed in a fish; and severe activity which would approach or equate to the sprinting effort in man. It is the severe activity which results in death. However, most of the activity of a fish probably consists of moderate activity such as the normal cruising rate.

It is also useful to correlate the degree of muscular activity with the behaviour of the fish. Thus far very little work has been done in this area. In the work that has been done on muscular fatigue in Kamloops trout yearlings, three correlates of behaviour are identified with fatigue. These are a reduction in the maximum swimming speed: the breakup of schooling behaviour where more than five or six fish are exercised together: and a change, in the pattern of the fish, from an effort to escape by rapid swimming to an effort to evade the capture by seeking dark corners (Black, 1957a).

As a prelude to discussing the papers in Table I, a brief outline of the important biochemical changes following muscular activity will be presented

[1]Received for publication February 28, 1958.

[2]A paper read at the 11th Meeting of the Canadian Committee on Freshwater Fisheries Research, at Ottawa, January 3, 1958, by Professor F. E. J. Fry.

J. Fish. Res. Bd. Canada, 15(4), pp. 573–586, 1958.
Printed in Canada.

TABLE 1. Comparison of mortalities in fish following severe muscular exertion.

Author and date	Place and year of study	Species and environment	Type of exercise	Total number of fish	Percentage mortality
von Buddenbrock, 1938	Heligoland, Germany 1936–7 and Naples, Italy, 1937	Cod, *Gadus morrhua*, and dab, *Platessa limanda*, in sea water	Struggling in live-box	—	—
Secondat and Diaz, 1942	France, before or during 1942	Tench, *Tinca tinca*, in fresh water	15 minutes vigorous chasing	10	20
Litt, 1954	Tracy, California 1952–53	Striped bass, *Roccus saxatilis*, in fresh water	Swimming to avoid fish screen	1,782	25
Anonymous, 1957	Tracy, California 1954–1956	Striped bass, *Roccus saxatilis*, recovery in fresh water	Maintaining position in turbulent flow	3,485	20.2
	" "	Striped bass, recovery in salt water	"	10,837	10.6
	" "	Chinook salmon fingerlings, *Oncorhynchus tshawytscha*, in fresh water	"	5,291	19.3
Black, 1957c	Nanaimo, B.C. 1956	Sockeye salmon, *O. nerka*, hatchery raised, 2 years old, 7-oz., in sea water	15 minutes vigorous chasing	19	25
Parker and Black, MS	Cape Fairweather, Alaska, 1957	Chinook salmon, non-migrating, 8-lb., in sea water	Swimming and struggling on a troll line	60	37

(after Mommaerts, 1950). Most important amongst the compounds involved is the contractile protein. Probably magnesium and other metallic ions such as sodium are essential in the activation process of the contractile protein. When the energy-rich adenosine triphosphate hydrolyses to release energy, phosphoric acid is liberated. Creatine phosphate is another energy-rich phosphate which is important in supporting the chemical changes of muscular activity. Creatine phosphate breaks down to creatine and phosphoric acid with the release of energy, but in these reactions the acidity is markedly less than is the case with the adenosine triphosphate change. The next important group of compounds include glycogen and the many carbohydrate intermediaries till finally pyruvic acid is produced as a result of the breakdown of glycogen. In the presence of oxygen, the pyruvic acid oxidizes through the so-called citric acid cycle to release great quantities of energy. If oxygen is not present then the pyruvic acid breaks down to lactic acid with very much less energy released. The appearance of lactic acid is correlated with an increase in acidity. Pyruvic and lactic acids may, of course, be resynthesized to glycogen through the Embden–Meyerhof chain of reactions, but the probable route in mammals at any rate is a conversion of lactic acid to glucose in the liver; thence, as glucose, to the muscles where it may change to glycogen (Cori cycle). Lactic acid may also be metabolized by the heart muscle and excreted by the kidneys. Some workers in mammalian physiology claim that glycogen breaks down to lactic acid only in the marked absence of oxygen. Other workers claim that lactic acid is produced with every contraction.

In the foregoing, death following severe muscular activity has been ascribed to the injurious effects of metabolites produced during the chemical release of energy. It is also possible that death could occur from the failure of an adequate store of chemical reserves, especially that of glycogen.

RESEARCH ON HYPERACTIVITY AS A LETHAL FACTOR IN FISHES

The first observations on muscular exertion as a cause of death in fishes were made by von Buddenbrock (1938).

In 1936, while working at the Biological Station at Heligoland, he observed that the blood of cod and flatfish held in the Aquarium was very dark and did not brighten even when placed in air. He also noticed that the cells were deformed. In 1937 he studied the problem both at Naples and again at Heligoland. He studied both the cod and a flatfish and observed that the blood of dying fish did not take up oxygen as contrasted with the blood of fresh fish. The dying fish had been struggling in captivity. Von Buddenbrock attributed the reduction of oxygen-combining power of the blood and the deformity of the blood cells to the presence of lactic acid which had been caused in the first instance by muscular activity (Table).

Huntsman (1938) reported that he was able to keep herring and haddock alive in aquaria when, upon capture, the struggling of the fish was reduced to a minimum. Huntsman attributed the death in struggling fish to lactic acid production which in turn caused asphyxiation of the fish. This work was done at the

Atlantic Biological Station of the Fisheries Research Board of Canada, St. Andrews, New Brunswick.

Secondat and Diaz (1942) were the first to show that, for tench, the blood level of the lactic acid increased following vigorous activity and then continued to increase during the recovery period for as long as 6–8 hours. They also showed for certain fish which did not survive, that the blood level of lactic acid failed to subside after 6–8 hours. The important work of these authors is, however, open to two points of criticism, namely that not very many experiments were conducted and secondly, that blood samples were taken repeatedly from the same fish. No control fish was subjected to fatigue and then allowed to recover (Table).

Litt (1954), and Bates and Vinsonhaler (1957), working at the Tracy Pumping Station in the delta of the Sacramento and San Joaquim rivers, reported death of striped bass following prolonged swimming to avoid fish screens. Detailed results for mortality of striped bass have been reported by Bates, Vinsonhaler, and their colleagues in an anonymous report published in 1957. Out of 3,485 fish, 704 or 20% died during recovery from muscular fatigue resulting from traversing a fishway. The fish were placed in untreated canal water. In a similar experiment, mortalities fell to 10.6% (1,152 out of 10,837) when recovery took place in salt-treated canal water (Table). The salt-treated fish were subjected to the additional hazard of transportation by truck. Litt (1958) emphasizes that the striped bass and chinook salmon were subjected to mechanical injury during the operations of capture, handling and transportation.

During the summers of 1956 and 1957, De Lacy and Paulik (1958) tested the swimming capacities of adult migrating sockeye salmon from the Columbia river. In 1957 there were 6 mortalities from a total of 168 fish tested at the McNary dam; 4 mortalities out of 252 tested at Rock Island dam; and no losses out of 48 tested from the Tumwater dam in spite of the fact that the fish were hauled from Tumwater dam to Rock Island dam for testing. De Lacy and Paulik hold the opinion that such losses as occurred were possibly due to mechanical injury including loss of scales, rather than from the effects of muscular exercise.

Black (1957c) experimented on sockeye salmon that had been in fresh water for their first 6 months and then in sea water for the 18 months previous to the study. Following vigorous activity for 15 minutes, the salmon were allowed to recover. Fish were taken from time to time and samples of blood drawn from the heart. During the recovery, however, 5 of the 19 individuals thus treated succumbed. The temperature of the water was 20°C. which is above the mid-point of the viable range, yet not up to sub-lethal temperature. It also should be noted that these were hatchery-raised fish. It is unlikely that any glycolysis had taken place as a result of *rigor mortis* before the blood samples were obtained. These observations on lactic acid content of the blood of fish confirm and extend the work of von Buddenbrock (1938).

During August of 1957 samples of blood were taken from chinook salmon that had been captured 15 miles off Cape Fairweather, Alaska (Parker and Black, MS). Some of the fish were sampled immediately after they had been caught by trolling. The remainder were transferred to a live-well in the hold of the boat

through which sea water was continuously pumped. Not more than 4 fish were held in the live-box at one time and usually there were only one or two fish held at one time. Fish were sacrificed from time to time and blood samples taken. As in the previous work just reported, fish died within the recovery period. Samples of blood were taken from these fish well before *rigor mortis* set in.

Parker and Black estimate that when consideration is given to the fish that were removed for sampling, the percentage mortality as a result of exercise would be 71%, as against the simple percentage of 37%. The recovery curve indicated that the pattern of lactic acid levels in the blood following the 14 minutes trolling was the same as that reported for the sockeye salmon blood (Black, 1957c). That is, the blood level of lactic acid continued to rise during the recovery period and did not subside for some 8 hours. Twenty-two out of a total of 60 fish expired during the recovery period. The average blood lactic acid of the 22 fish that expired was 184 mg.% or three times the value for the fish that had been just taken off the troll line. The objection may be raised that the live-well in a vessel at sea does not constitute an ideal or even an adequate holding facility to permit the recovery of the fish from the effects of muscular exercise. The fish did not struggle nor thrash about in the holding tank. All fish that were held for recovery were free from obvious wounds of any type. This work represents the first data obtained upon the effects of trolling upon subsequent recovery, as well as upon one chemical correlate of muscular activity, namely, the blood level of lactic acid. Moreover the work is in keeping in every way with the previous account of fish held in an experimental hatchery and exercised by chasing.

Smith (1955) discusses the problem of keeping the coelacanths alive. He notes that, when captured by spearing, in spite of the great loss of blood and other damage the coelacanth shows a better chance of survival than when captured on a hand line. Smith refers to the "common knowledge" of all deep-sea fishermen that fish caught on a hand line show a poor chance of survival. Smith attributed the adverse effects of capturing by hand line to the nervous excitement induced in the fish.

THEORIES REGARDING THE CAUSE OF DEATH

The foregoing experiments show that under certain conditions, death may follow severe muscular exercise on the part of the fish, and that at least one chemical correlate of muscular exercise, namely, lactic acid, is present in significantly high quantity when death occurs. However, severe muscular exercise will not always be followed by death in the immediate few hours following exercise. On the contrary, mortalities due to exercise alone were not observed in any of the controlled experiments carried out on Kamloops trout over four years of experimentation (Black, 1955, 1957a), nor in the lake trout (Black, 1957b). As reported above, DeLacy and Paulik (1958) did not observe any mortalities in Tumwater dam series of adult sockeye salmon and very few deaths in their other experiments. DeLacy and Paulik suggested that death in their experiments was due to mechanical injury.

Reduction in Oxygen Combining Power of the Hemoglobin by Lactic Acid

Von Buddenbrock (1938) observed that the blood in the gills of the fish which had struggled in captivity remained very dark. He appreciated the work of Green and Root (1933), in which the marked effect of acid in reducing the oxygen combining power of hemoglobin was demonstrated. Using the Barcroft method, von Buddenbrock demonstrated that the oxygen capacity of the blood of fish which had been exercised was reduced from initial 100% to 33–61% saturation in fish dying from struggling. A reduction in oxygen capacity of the blood of carp from 100% to 62.5% saturation, following 15 minutes of vigorous muscular activity, was demonstrated by Secondat (1950).

It has been known for decades that acid will greatly increase the volume of red cells (Ponder, 1948). Black and Irving (1938) showed that for the blood of the white sucker *Catostomus commersoni* not only was the oxygen combining power greatly reduced by lactic acid in *in vitro* experiments, but that the lactic acid finally burst the red cells. The concentration of lactic acid at which the destruction of the red cells occurred was 400 mg.%, or over twice that observed in the blood of the dying sockeye salmon (Black, 1957c) or the dying chinook salmon (Parker and Black, 1958). However, there is no evidence that the reduced oxygen capacity is not sufficient to provide oxygen for metabolism until direct experiments are carried out. The theory that acid metabolites cause reduction in oxygen capacity sufficient to cause death by hypoxia can neither be disproved nor supported.

Alteration of Blood Lactic Acid, pH and Carbonate following Activity

Auvergnat and Secondat (1942) noted that the pH of carp blood at rest was 7.33 and immediately after exercise it was 7.25, at which level it remained for the first two hours and then rose to 7.31 at the end of six hours. In Figure 1 the pH changes of the blood in Kamloops trout during fifteen minutes of exercise and for the recovery period up to one half-hour are presented (Black *et al.*, 1958). On the same graph, changes in blood levels of lactic acid and carbonic acid are shown. It will be noted that the hydrogen ion concentration rose during the first six minutes. This is the interval during which the maximum swimming rate of the Kamloops trout declined precipitously. After six minutes of activity the pH changes in the other direction. Between half an hour and one hour of recovery, however, the acidity goes up again, then declines at the sixth hour, to slowly increase to the point that approaches the initial resting level. These latter changes are shown on Figure 2. It will be noted that the first change in hydrogen ion concentration is correlated with initial rise in the carbon dioxide level of the blood. The second rise in hydrogen ion concentration is actually accompanied by a significant drop in carbon dioxide level and a marked increase in the lactic acid concentration. The second decline in hydrogen ion concentration is accompanied by a decline in lactic acid and a gradual increase in the carbon dioxide level back to somewhere near the initial resting position. Auvergnat and Secondat (1942) also studied the carbon dioxide level of the blood and found a decrease im-

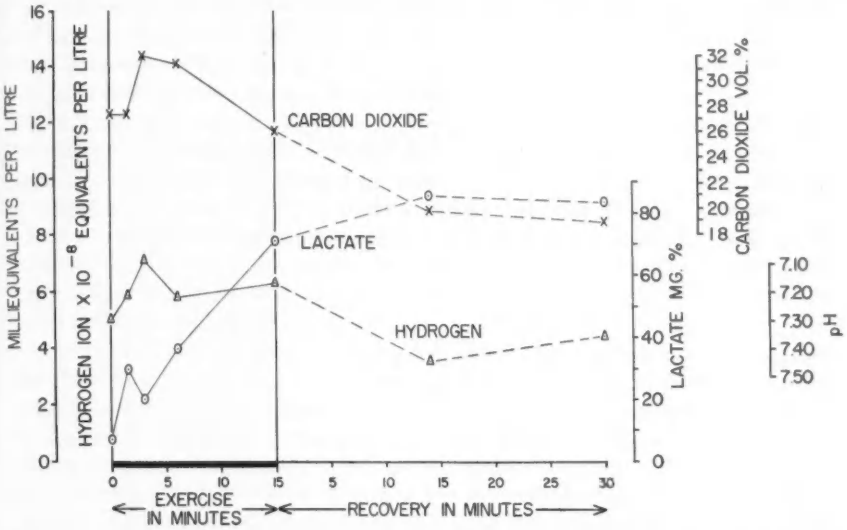

FIG. 1. Changes in blood levels of carbon dioxide, hydrogen ion and lactate for yearling Kamloops trout during 15 minutes of vigorous exercise and 30 minutes post-exercise recovery. 1957. 11.5°C. From Black *et al.*, MS, 1958.

mediately following muscular activity. This was accompanied by a slight further decrease during the recovery period up to six hours.

It would appear that there are two rises in the hydrogen ion concentration of the blood. The first rise is associated with a decline in the maximum swimming rate of the fish and an increase in the carbon dioxide content of the blood long before the lactic acid level has reached its maximum point, but not of course before the lactic acid itself has begun to rise. The second rise in hydrogen ion concentration is usually no greater than the pH at rest. This occurs during the recovery and at a time when the carbon dioxide level has dropped to nearly its lowest point. If fish die because of severe muscular activity, they appear to die during the recovery period, some time after the first half-hour. Yet at this interval the hydrogen ion concentration is not greatly increased beyond the normal, if increased at all. Death appears to occur, however, when the carbon dioxide level is down and the lactic acid level is up. Whether the death is associated with a marked loss in the alkali reserve of the blood remains for future experimentation to determine.

An interesting feature of the hydrogen ion concentration is the rapid fall after the sixth minute of activity down through to the remaining 15 minutes of muscular activity, and then on to the first 10 minutes of post-exercise recovery. Nakatani (1957) has shown that there is a significant increase in inorganic phosphate both in blood plasma and muscle tissue in adult steelhead trout immediately

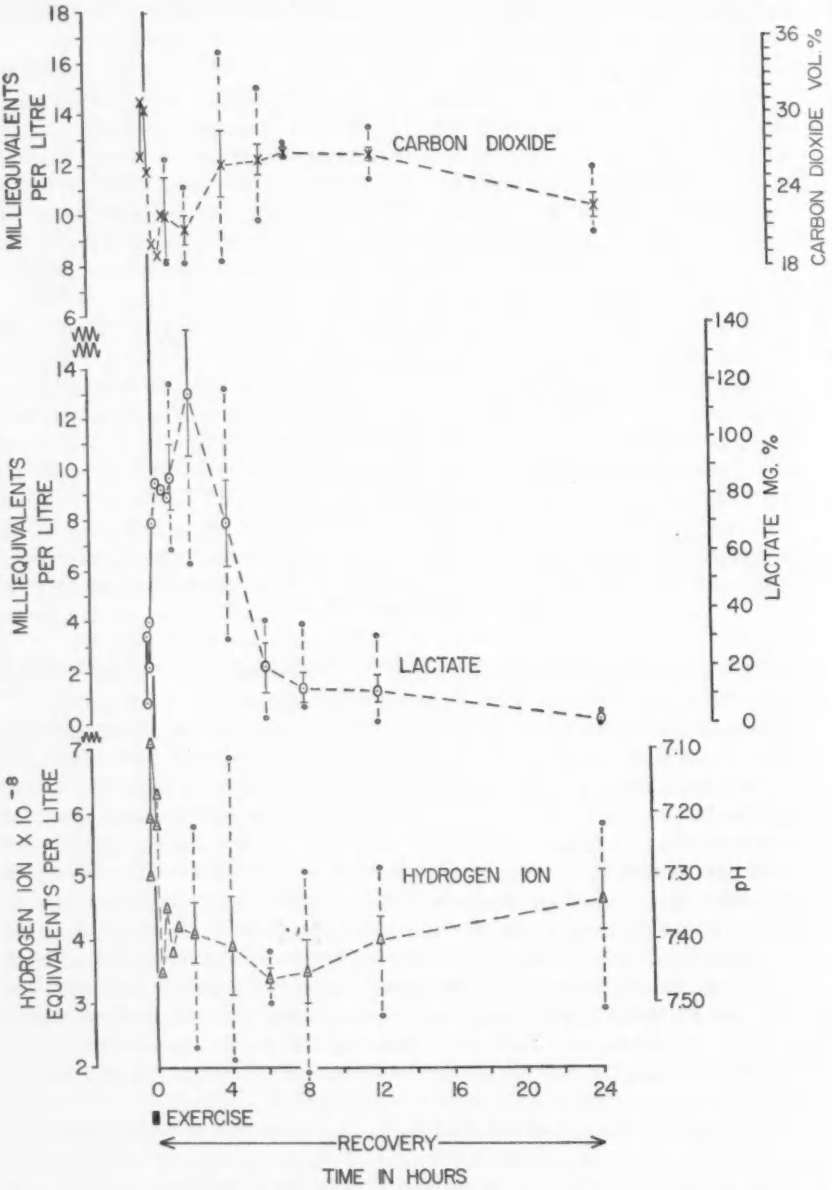

FIG. 2. Changes in blood levels of carbon dioxide, hydrogen ion and lactate for yearling Kamloops trout during 15 minutes of vigorous exercise and 24 hours post-exercise recovery. 1957. 11.5°C. From Black *et al.*, MS, 1958.

following strenuous exercise. Felton (1956) has shown that there was a significant increase in creatine and inorganic phosphate in steelhead trout following exercise. As was shown by Dubuisson (1939) the hydrogen ion concentration of muscle first increases, then decreases, then increases again. These changes in hydrogen ion concentration are correlated with first an increase in the concentration of phosphoric acid following the hydrolysis of the initial adenosine triphosphate molecule; next, a fall of hydrogen ion concentration accompanying the hydrolysis of creatine phosphate; next, a gradual increase in hydrogen ion concentration which accompanies the appearance of lactic acid. Whether or not creatine appears in the blood, the production of the relatively more alkaline creatine in the muscle could influence the course of the hydrogen ion concentration both in muscle and blood in the downward direction.

So far as the hydrogen ion changes in the blood are concerned, it appears that there is no correlation between the maximum increase in hydrogen ion concentration and the time of death of the animal. Either we must admit, then, that the hydrogen ion increase is not the primary cause of death, or that there is a hydrogen ion increase in tissues that is not reflected in changes in the blood. The one correlation of increase in hydrogen ion concentration in the blood which is positive, however is the increase in hydrogen ion concentration initially that accompanies the marked reduction in the maximum swimming speed of the fish. It is also possible to argue that the reduction of maximum swimming speed is likewise due to the decrease in energy rich phosphorous compounds serving the contractile process.

Litt (1954) and Bates and Vinsonhaler (1957) demonstrated that there was a significant reduction in mortalities when fatigued salmon and striped bass were allowed to recover in fresh water to which salt had been added. Black (1957c) found that yearling sockeye salmon, raised and held in fresh water, responded to fatigue in the same way as did Kamloops trout (Black, 1957a; Black *et al.*, 1958) and lake trout (Black 1957b) when exercised in fresh water. When, however, the sockeye salmon yearlings were transferred to sea water for 48 hours and then exercised, the response differed. The lactic acid in the blood had fallen to a low level in the two hours following fatigue, instead of rising. The fish in salt water could scarcely be fatigued. Moreover, it seemed very easy to draw blood from the heart following exercise in salt water, indicating that the action of the heart was actually increased by exercise. The benefit of a salt environment following fatigue (Litt, 1954; Bates and Vinsonhaler, 1957; Black, 1957c) may be explained as follows: the salt may have restored osmotic balance which Auvergnat and Secondat (1942) showed was altered by exercise in the carp; salts necessary for muscular activity may have crossed the gill membrane; the most likely explanation is that hydrogen ion from the blood may have been exchanged for sodium or some other metallic ion. At the moment it is mysterious that significant mortalities occurred in sea water (Black, 1957c; Parker and Black, 1958). It would appear that the fish living in sea water is unable to use the rich alkaline buffering mechanism of the sea water to cope with the increase of acid in the tissues following severe exercise. Equally mysterious is the fact that adult salmon returning

to fresh water appear resistant to immediate death following vigorous muscular exercise (De Lacy and Paulik, 1958).

A few words of explanation may be given about the prolonged period necessary before disappearance of lactic acid from the blood following exercise in fishes. In man, the decline in the blood level of lactic acid begins as soon as the severe exercise is ended, or acid may increase for ten minutes and then subside (Bang, 1936; Crescitelli and Taylor, 1944). The return of lactic acid to approximately the resting level was complete in 50–60 minutes in these experiments on man. In fish, however, the lactic acid increases immediately in response to the vigorous exercise and then continues to increase for the first one to four hours following recovery. Indeed the lactic acid does not decline to near resting levels until anywhere from the eighth to twelfth hour of rest after exercise. There are three possible reasons why lactic acid may continue to increase and take so long to disappear in a trout and salmon. The first and most important, based on the work of Johnson, Edwards, Dill and Wilson (1945), is that lactic acid diffuses very slowly at lower temperatures. The second reason may be that the liver and other organs and tissues which may utilise or excrete lactic acid, may fail to function rapidly, again because of the lower diffusion rate. A third possibility is that the rate of circulation may be seriously reduced by the effect of acid upon the heart (Redfield and Medearis, 1926). These three factors may be operating together at the same time.

Depletion of Energy Reserves

In considering the possibility that the reserves of energy may be depleted in an exhaustive effort, it is at the moment impossible to distinguish whether the energy precursors, etc., have not yet been resynthesized or whether the acid has not been adequately neutralized.

It is possible that the death of the fish following muscular activity is due to a complete exhaustion of the fundamental primary energy stores such as the high energy phosphate compounds adenosine triphosphate and creatine phosphate, and the carbohydrates, particularly glycogen and all the intermediate compounds including pyruvic acid. Felton (1956) has measured the increase in creatine and inorganic phosphate following exercise in three-year-old steelhead trout. Nakatani (1957) has followed the increase in inorganic phosphate and also lactate in muscles immediately following exercise of steelhead trout. As yet, however, no study appears to have been made indicating the degree of depletion of the initial primary stores of adenosine triphosphate, creatine phosphate and glycogen. Many of these compounds are so labile that it is technically difficult to obtain the information. At the present time, then, nothing can be concluded concerning the possibility that the primary stores of chemical fuel have been exhausted immediately following vigorous exercise.

Not many analyses of muscle glycogen in fish are available. From the data thus far published it would appear that the level of glycogen is about one-tenth of that in mammals. Under certain conditions the low level of glycogen in fish muscle is, nevertheless, capable of providing enough lactic acid to swamp the

buffering mechanisms and thereby possibly be the cause of death. If the glycogen level in fish muscle was consistently as high as that found in mammalian muscle, then presumably severe muscular exercise would invariably cause death. It is tempting to suggest that there is a teleological association between the low storage level of glycogen in muscle of fish and the fact that death may result if fish are vigorously exercised under certain conditions.

One method of investigating the relation of the restoration of chemical reserves and restoration of the pH would be to measure the time necessary for fish to completely recover from an exhaustive swimming effort. This very experiment has been performed by Paulik and De Lacy (1957) for adult steelhead trout in which they showed that recovery had occurred after 6 hours.

Possible Deleterious Effects on the Fish of Muscular Fatigue Products

There is some scanty evidence that the cardiac activity of trout is reduced by the vigorous muscular exercise (Black, 1957a). The evidence is based largely on the difficulty in obtaining blood samples by cardiac puncture after exercise and during the recovery from exercise, as compared with blood taken from unexercised fish. These observations are substantiated to a degree by electrocardiographic readings taken on trout. No electrical recording was registered for two fish out of eight following severe exercise. The conclusion was reached that the heart activity had stopped. Redfield and Medearis (1926) showed that the efficiency of the exercised heart of turtle decreased directly as the concentration of lactic acid was increased. It is possible, then, that the cardiac activity of the heart is impaired by fatigue products. Whether this is due to reduction in the efficiency of the contracting heart (smaller stroke volume) or a reduction in the rate of heartbeat cannot be settled at the present time for most of the evidence shows that the heart rate actually increases as a result of exercise.

As is well known the activity of the heart of fish is directly linked with the activity of the respiratory system. Death in the fish following vigorous activity was commonly preceded by respiratory distress and occasionally gasping breaths prior to cessation of breathing. On the other hand, the initial effect of exercise is to increase the respiration rate.

Another sign of death or the imminence of death in fishes that had been severely exercised was their loss of orientation in swimming. They either swam on their sides or ventral side up for a while before death occurred.

At the present time the precise cause of death resulting from muscular activity in fishes is not known. In time, death occurs one-half to three hours following muscular activity during which interval the lactic acid of the blood is very high and the blood level of carbon dioxide is at its lowest point. Nevertheless the pH of the blood appears to be indifferent during this period. Immediately preceding death there is commonly an upset in the orientation of the animal and a spasmodic breathing pattern is apparent. While von Buddenbrock (1938) and also Secondat (1950) have reported reduction in the oxygen carrying capacity of the blood due to the acid produced following fatigue, we do not know that this reduction in oxygen capacity is the significant cause of death. Von Buddenbrock

has also described change in the shape of the red blood cells in fatigued fish and Black (1956) has reported the occasional formation of soft clot following fatigue.

For want of a more precise description we may conclude that death in fishes is a result of a combination of adverse factors as yet not completely described. It is clear that the problem of what causes death following the vigorous activity will not be settled until more experiments are carried out on fish that die in response to muscular activity.

SUMMARY AND CONCLUSIONS

1. Death occurs in fishes under certain circumstances following severe muscular activity. The conditions described include struggling in a live box, responding to vigorous chasing, swimming through swift passages of water, and struggling on a trolling line. Death has been observed under these conditions both for fishes such as salmon, striped bass and shad in fresh water, and fish such as two-year-old sockeye salmon, nearly mature chinook salmon, and codfish and flatfish in sea water.

2. The precise cause of death is not yet known. However, it is likely that the severe acid-base disturbance following the large accumulation of lactic acid may be the principal cause of death. In any case the acid concentration is sufficient to reduce the oxygen combining power of the blood, reduce the alkali reserve or carbon dioxide combining capacity of the blood and alter the shape and probably volume of the red blood cells. There appears to be a marked reduction in the ability of the heart to pump blood following severe exercise. The ability of the fish to maintain an upright position and the respiration are commonly disturbed immediately prior to death.

3. Severe muscular activity rapidly reduces the maximum swimming capacity of trout. Other changes in behaviour were noted, namely the failure of fish to swim in a school shortly after vigorous activity; and a change from evading the chaser by rapid swimming to a pattern of seeking out dark corners to avoid capture.

4. The importance of severe muscular activity to the study of biology and especially of the physiology of fishes is clear. Both the oxygen and carbon dioxide carrying capacity of the blood must be profoundly altered by accumulations of fatigue products. The question of oxygen debt must also be considered following a history of activity in fishes.

5. Hyperactivity as a lethal factor in fishes is of very great significance in problems of fisheries management. The consequence of severe muscular activity is important in every aspect of handling of fishes, for example, live transport of fishes, tagging, construction of fishways, etc.

ACKNOWLEDGMENTS

This paper was prepared at the suggestion of Professor F. E. J. Fry for presentation to the Symposium on tolerance limits of freshwater fish convened by the Fisheries Research Board of Canada in Ottawa, Canada, on January 3, 1958. Generous assistance was rendered by the following who gave results of their work

prior to publication: Dr. Daniel W. Bates, Dr. Russell Vinsonhaler, Mr. Bertram D. Litt, Dr. Allan De Lacy and Mr. Gerald Paulik. The careful criticism of the manuscript by Dr. Casimir C. Lindsay is appreciated.

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The Effect of Temperature on the Cruising Speed of Young Sockeye and Coho Salmon[1, 2]

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ABSTRACT

The cruising speeds of underyearling and yearling sockeye and coho salmon were determined in a rotating annular trough, for acclimation temperatures ranging from 1° to 24°C. Variation in swimming speed characterized the first 40 to 50 minutes; subsequently a relatively steady state was obtained.

Optimum cruising speeds occurred at 15°C. for sockeye and 20°C. for coho. Maximum sustained levels fell mainly between 1.0 and 1.5 ft. per second (30 and 45 cm. per sec.).

Exercised young coho showed improved performance over those raised in standard hatchery troughs.

The significance of the relative swimming capacities of the two species, and the effect of temperature, is discussed in relation to their ecology.

INTRODUCTION

In a study of the lethal temperatures of five species of Pacific salmon (genus *Oncorhynchus*), Brett (1952) was able to demonstrate small but significant differences in heat tolerance, for comparable stages of thermal acclimation. These differences, at most, did not amount to more than 0.7°C. in the case of coho (*O. kisutch*) and sockeye (*O. nerka*). At the time it appeared that relatively slight differences in temperature tolerance could hardly be responsible for the marked distinctions in freshwater distribution of some of the species. Young coho and sockeye occupy separate freshwater zones which differ in relation to such gross features as mean depth, water velocity, food, and temperature. It appeared, therefore, either that physiological response to temperature was not the major influencing factor governing distribution, or that some other functional relation was involved, of more pronounced significance than that directly reflected by the lethal temperatures.

Fry (1948) has reported that chars (*Salvelinus*) and trout (*Salmo*) show basic differences in their *swimming-rate* versus *temperature* curves, and this observation has been supported by a comparison of the standard and active metabolic rates (Graham, 1949). Brett (1956) in reviewing the thermal requirements of fishes states that "if this relation of activity to temperature has survival value, cases in which similar or nearly similar lethal temperatures exist, accompanied by dissimilar peaks for maximum activity, might be expected to have different distributions according to temperature, under otherwise relatively similar habitat conditions". The species in the genus *Oncorhynchus* with their

[1]Received for publication February 20, 1958.

[2]A paper presented at the 11th Meeting of the Canadian Committee on Freshwater Fisheries Research, at Ottawa, January 3, 1958.

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J. Fish. Res. Bd. Canada, 15(4), pp. 587–605, 1958.
Printed in Canada.

comparable lethal limits provided an excellent opportunity to examine this thesis, particularly for the two species, coho and sockeye.

Another objective prompted this investigation. The sustained swimming speeds of fish, and the influence of temperature, are little known (Gray, 1957). When the problem of how to guide salmon safely around obstacles became acute because of the building of high dams on salmon streams, it was important to determine what velocity of water young migrants could stem without being swept to destruction. The absolute level of performance, as well as the comparative study of swimming speeds, was consequently of considerable interest.

MATERIALS AND METHODS

Apparatus

An annular trough, similar in conception to that described by Fry (1948) but somewhat enlarged and modified, was employed (Fig. 1 and 2). The circular trough itself was 40 inches (102 cm.) in outside diameter consisting of an open annular ring, 4 inches (102 mm.) wide and 5 inches (127 mm.) high, made of ¼ inch (6.3 mm.) Lucite with seams carefully ground and cemented to minimize moving visual cues. When filled to the operating level, 25 mm. from the top, it contained 31.5 litres.

A ¼ horsepower motor linked to a Zero-Max torque-converter provided a readily adjusted source of power. An encircling outer screen, coaxially mounted on the central shaft, was marked with black stripes (½ inch or 13 mm. wide) on a white background. A lower deck, immediately under the annular trough and on the same mounting as the screen, was marked in a like manner. The balance of the visible environment for the fish was painted a flat black. Immediately above the centre of rotation and suspended from the ceiling, 6 feet from the trough, shone a cone of light. The perimeter of the light cone was adjusted to illuminate the trough and outer screen only, leaving the observer in relative darkness. A variable transformer in series with the light allowed control of intensity of illumination, which was usually between 2 and 3 foot-candles, but was occasionally reduced to 0.2 ft.-c. for a fish that showed a tendency to dive. In general, strict observance of quiet, of reduced lighting, and careful acceleration of the rotating trough was found necessary to obtain steady, unerratic behaviour. Despite these precautions about one-tenth of the fish had to be eliminated because of inconsistent behaviour.

Fish

Two species and two age-groups of young Pacific salmon were tested: coho and sockeye, as underyearlings and yearlings (Table I). The fish were raised from eggs taken from local wild stock—the coho from Nile Creek, Vancouver Island, the sockeye from Hooknose Creek, near Port John, King Island. They were kept in standard-type hatchery trays and long rectangular troughs throughout culturing. One exception to this standard procedure was introduced in the case of exercised fish. In this instance, a circular culture tank was used, 40 inches (102 cm.) in diameter, containing 500 litres of circulating water. The velocity at

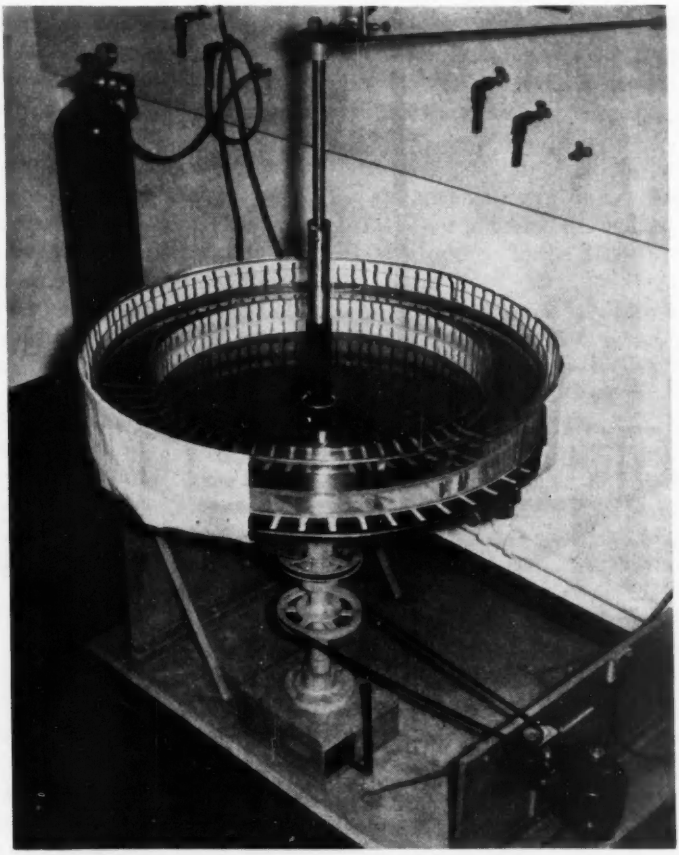

FIG. 1. Photograph of annular trough coaxially mounted with outer "visible screen". The drive mechanism for the trough appears in the bottom right-hand corner.

the perimeter of the spiralling water (central drain) was approximately 0.8 foot per second (24 cm./sec.). Fish were free to move anywhere within the tank but usually occupied a position in the outer half.

TABLE I. Mean fork length and weight, standard deviation in length and weight, test times, and ages of the sockeye and coho salmon used in cruising speed determinations.

Species and age	Length	Weight	Test times	Age
	cm.	*g.*		*months*
Sockeye underyearlings	6.95±0.77	2.90±1.09	June 11–Aug. 12	4–6
Coho underyearlings	5.45±0.74	1.67±0.74	June 24–Aug. 13	4–6
Sockeye yearlings	14.47±0.81	30.91±6.44	Aug. 18–26	18
Coho yearlings	8.93±0.74	8.09±1.61	Jan. 19–Mar. 15	11–13

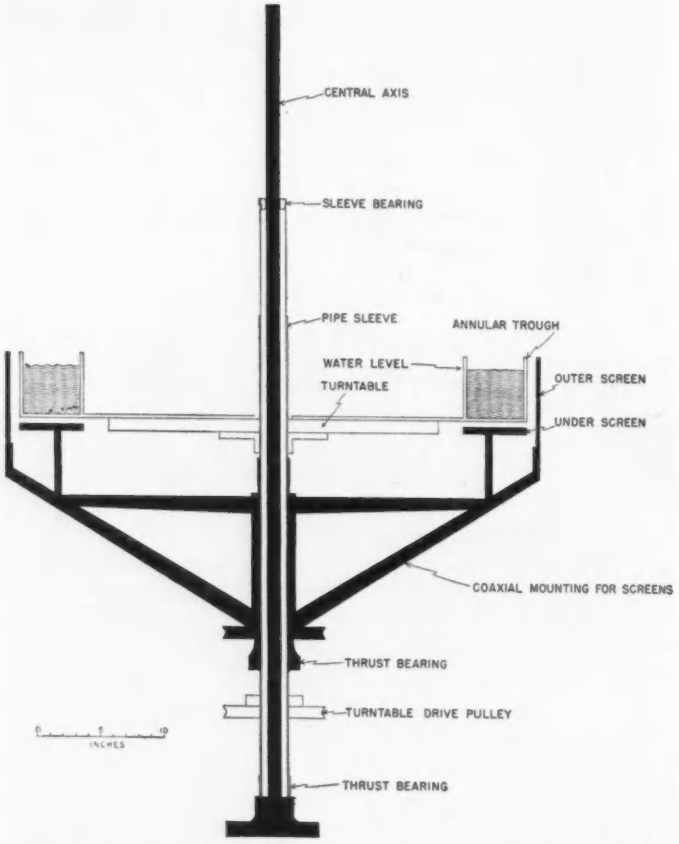

FIG. 2. Diagram of annular trough. Outer coaxially mounted screen is shown in black. This remained stationary during cruising speed tests.

With but few exceptions, five fish were tested individually at each of five acclimation temperatures. The combination of time to perform a single test, the number of species, acclimations, and ages resulted in some weeks elapsing between the start and finish of a given series. Growth in the stocks occurred, differentially at different acclimation temperatures. The ideal experiment would involve only one size for all acclimations. An attempt to bring the performance curves to a common denominator has been made by determining a growth correction factor (see Fig. 5).

TEMPERATURES

EXPERIMENTAL. The temperature of the rotating trough was maintained within approximately $\pm 0.5°C.$ of the prescribed acclimation temperature. This was achieved by commencing an experiment with the temperature 0.5° lower

than the acclimation level and partially flushing with cold water when the temperature had risen to 0.5° above the desired level. Rotation was not stopped for this exchange. In many instances no addition of cold water was necessary during the time of a run since the differential between water and air temperatures was kept to a minimum.

ACCLIMATION. Acclimation temperatures of 1°, 5°, 10°, 15°, 20°, 22° and 24°C. were employed, though not all for any given species or age. Minimum acclimation times prescribed by Brett (1952) were imposed, as well as periods of up to two weeks in excess of these times. Variations from the defined temperature levels rarely exceeded ±0.5°C.

It was found impossible to hold the trough temperature down to 1°C. for this acclimation temperature. A test temperature of 2° to 2.5°C. was obtained. The data have therefore been plotted at the intermediate level of 1.75°C. in Figures 6 and 7.

Oxygen Levels

Water samples were taken for standard Winkler titration at the end of representative tests in each acclimation series. The relatively large volume of water, exposed surface, and additional feature of periodic flushing never resulted in less than 84% saturation, and averaged 92.3%.

Velocity Recording

In a smooth-walled trough such as the one employed, there was a large slippage factor at the start of rotation. This relation gradually approached an equilibrium state at some slight slippage ratio which made the direct calibration of the trough rotation an inaccurate record of the water velocity. To avoid this problem, a small circular plastic disc, radially edged with needle tips, was floated on the water surface. Free of frictional drag from the rotating wall, it provided an accurate direct measure of water velocity. This was confirmed by multiple tests with drops of dye.

Experimental Procedure

Fish were not fed on the day of an experiment, the time lapse amounting to 18 hours from the last feeding. Using a small nylon net a single fish was quickly dipped into a glass beaker and transferred in water to the annular trough. A period of 15 to 30 minutes was allowed for the fish to settle down, under reduced illumination. Subsequently, slow rotation was commenced, increasing the rate by regular increments every 5 minutes and raising the illumination slightly if the fish showed no erratic behaviour.

Stimulation to swim in the rotating chamber was provided by the fixed visual screen (pseudorheotropism) and was supplemented by tapping the edge of the trough at one point or, if this was insufficient, by touching the tail of the fish with the tip of a slender glass probe, long enough not to reveal the observer's hand in the cone of light. An attempt was made to apply the same intensity and duration of stimulus for each fish, by touching no more than twice on any given

round. The rotation rate was increased until a fish began to lose about one round in ten revolutions of the water mass, adjusting the rate to maintain this relation so that a continuous record of the maximum sustained swimming rate could be traced in 5-minute intervals. Early runs which were 40 to 50 minutes long were later extended to as much as 6 hours in an effort to obtain a consistent measure and to provide a definition of the *cruising speed* appropriate for these rather sensitive, active fish.

During each 5-minute interval a record of the radial position of the fish was kept, since the difference between the greatest inside and outside paths (allowing for free swimming) could amount to a 15% error.

RESULTS

Preliminary Tests

The first tests, conducted on yearling coho, showed a marked variability in swimming speed during the 50-minute period of trough rotation. The pattern was fairly consistent, but did not allow an appropriate assessment of the cruising speed since the swimming rate was subject to continuous change (Fig. 3). Relatively long-term tests were therefore introduced, as stated above, providing swimming distances of up to 4 miles (6.5 km.). Results from two of these tests are depicted in Figure 4. The early variability was followed by a prolonged stability in swimming performance, involving small oscillations around a mean

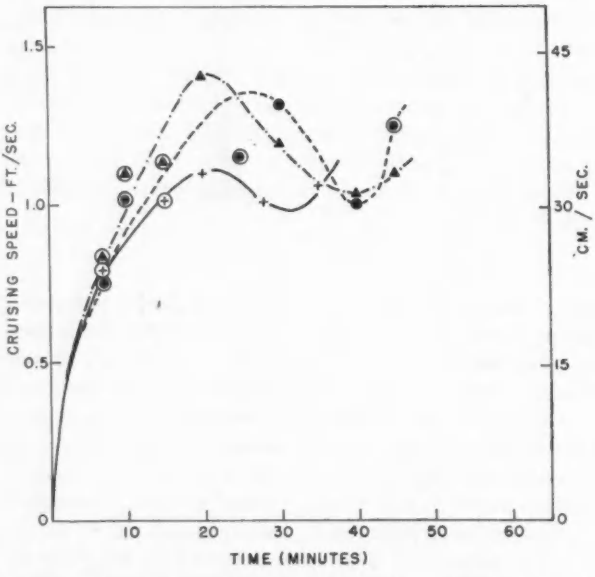

Fig. 3. Swimming speeds of 3 yearling coho acclimated to and tested at 20°C. Circled points represent rates at which the fish did not lose ground and were not necessarily making maximum effort.

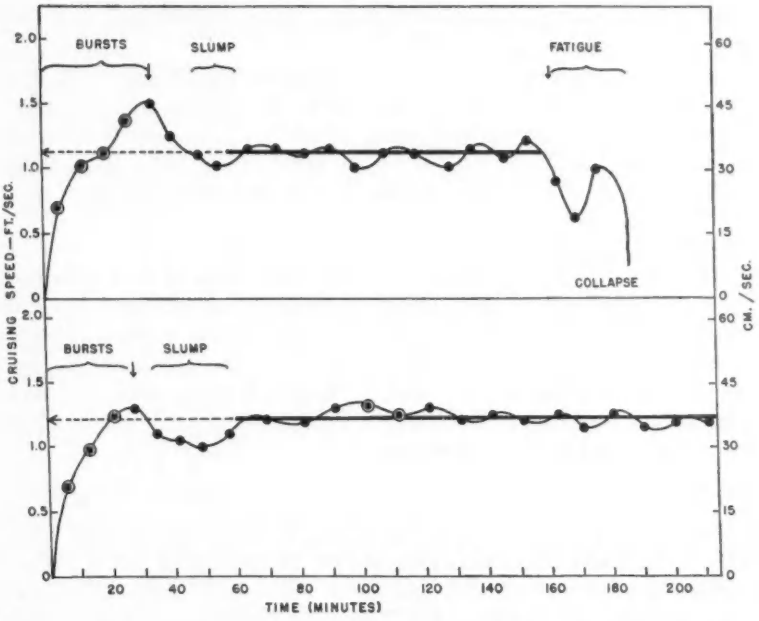

FIG. 4. Performance curves for two 15°C.-acclimated coho yearlings (*upper*, 9.0 cm., 8.2 g.; *lower*, 9.2 cm., 9.1 g.). Period of frequent bursts is indicated, terminating at the arrow. The solid line represents the cruising speed as defined in the text. Circled points as in Figure 3.

rate, given that fatigue did not occur. An effort was constantly made to ensure that a fish was exhibiting maximum sustained performance so that the full capacity to swim was displayed. This meant that fatigue could be produced if over-stimulation was applied, but offered a continuous record of the full capacity of the fish when carefully tested.

During the first 20 to 40 minutes following the start of the tests, when the rate of trough rotation was increasing, frequent rapid darts or short bursts of swimming accompanied the cruising rate. The darts were only 2 to 3 feet (0.7–1 m.) in length, at a comparatively high speed, probably 4 to 5 feet per second (about 1.4 m./sec.). As long as these persisted it was possible to increase the water velocity, resulting in the peak performance characteristic of the build-up period. Subsequent to this phase a slump in performance occurred, unless nearly an hour was spent in more gradual increase of the rate of trough rotation, in which case the fish were found to move directly into sustained performance.

From these preliminary tests the cruising speed was defined as: the swimming speed which a fish can maintain consistently for a minimum period of 1 hour under strong stimulus without gross variation in performance. This usually required an introductory period of 40 minutes or more, which either passed through

or eliminated the periods involving swimming bursts and slumps, and did not occasion fatigue or collapse.

It is interesting to note that when visual stimulus was allowed to be the only source of motivation for swimming a decrease in the net rate occurred. This supports the need for additional motivation which has been employed by others when determining maximum rates of oxygen uptake (Fry, 1957; Basu, 1957), or the performance of adult salmon (Paulik, DeLacy and Stacy, 1957).

Cruising Speeds

Following the procedure outlined, the cruising speeds of underyearling and yearling coho and sockeye were determined. These are summarized in Tables II and III for the various thermal acclimations. There was no particular difference in performance of the younger fish, with the exception that the bursts did not last as long. Given additional care not to cause fatigue, it was possible to obtain an hour's consistent performance following a shorter introductory period. Figures 6 and 7 illustrate the levels of performance.

Effect of Size

During the course of testing, as stated earlier, differential growth occurred in relation to time and acclimation temperature. In the case of the yearlings the circumstance of testing fortuitously resulted in rather small differences between the mean lengths of the samples tested. The longer period of growth afforded at more extreme acclimations was offset by the reduced growth rate. The difference in the underyearlings was proportionately larger.

Table II. Cruising speeds of coho underyearlings and yearlings tested at different acclimation temperatures, together with their standard deviations (S.D.) and standard errors of the means (S.E.). The last column gives the speeds adjusted to a common mean length by applying a correction factor of 0.094 ft. per sec. (2.8 cm./sec.) increase in cruising speed for a 1 cm. increase in length. The factor was determined from the mean slope of the lines relating length to speed, Figure 5.

Acclimation temperature	No. fish	Mean length	Mean weight	Mean speed	S.D.	S.E.	Adjusted speed	
Underyearlings								
°C.		*cm.*	*g.*	*ft./sec.*	*ft./sec.*	*ft./sec.*	*ft./sec.*	*cm./sec.*
24	5	6.34	2.52	0.93	0.13	0.06	0.86	26.2
22	1	6.80	3.00	1.23	...	...	1.10	33.5
20	5	5.60	1.90	1.00	0.14	0.06	0.98	29.8
15	5	5.70	1.72	0.83	0.06	0.03	0.80	24.4
10	6	4.85	1.35	0.72	0.10	0.04	0.77	25.5
6	5	4.62	0.67	0.49	0.06	0.02	0.56	17.1
Total	27	5.45	1.67					
Yearlings								
20	5	9.04	8.30	1.35	0.19	0.09	1.34	40.8
15	5	8.86	8.06	1.23	0.08	0.04	1.23	37.5
10	5	9.10	8.08	1.16	0.07	0.03	1.13	34.4
5	5	8.78	7.78	0.87	0.13	0.06	0.86	26.2
1	2	8.75	8.40	0.60	0.08	0.05	0.60	18.3
Total	22	8.93	8.09					

TABLE III. Cruising speeds of sockeye underyearlings and yearlings at different acclimation temperatures. The last column gives the speeds adjusted to a common mean length by applying a correction factor of 0.07 ft. per sec. (2.1 cm./sec.) increase in cruising speed for a 1 cm. increase in length.

Acclimation temperature	No. fish	Mean length	Mean weight	Mean speed	S.D.	S.E.	Adjusted speed	
°C.		*cm.*	*g.*	*ft./sec.*	*ft./sec.*	*ft./sec.*	*ft./sec.*	*cm./sec.*
Underyearlings								
24	5	7.36	3.44	0.71	0.18	0.08	0.68	20.7
20	5	7.36	3.36	0.89	0.17	0.08	0.86	26.2
15	5	7.10	2.82	1.07	0.07	0.03	1.06	32.3
10	6	6.23	1.94	0.88	0.06	0.02	0.93	28.3
10	5	7.64	3.92	0.88	0.09	0.04	0.83	25.3
6	5	6.64	2.86	0.75	0.09	0.04	0.77	23.4
1	3	6.17	1.67	0.47	0.05	0.03	0.52	15.8
Total	34	6.95	2.90					
Yearlings								
15	5	13.92	26.90	1.52	0.15	0.06	1.56	47.5
10	4	15.15	35.93	1.42	0.10	0.05	1.37	41.7
Total	9	14.47	30.91					

Bainbridge, as reported by Gray (1957), has found a more or less linear relation between swimming speed and length of fish for the same frequency of tail beat. Insufficient data were available to come to any such direct conclusion for young salmon. However, it was possible to determine an average increase in swimming speed for a unit increase in length by comparing the mean swimming rates for the two age-groups (Fig. 5). There are apparently differences in the

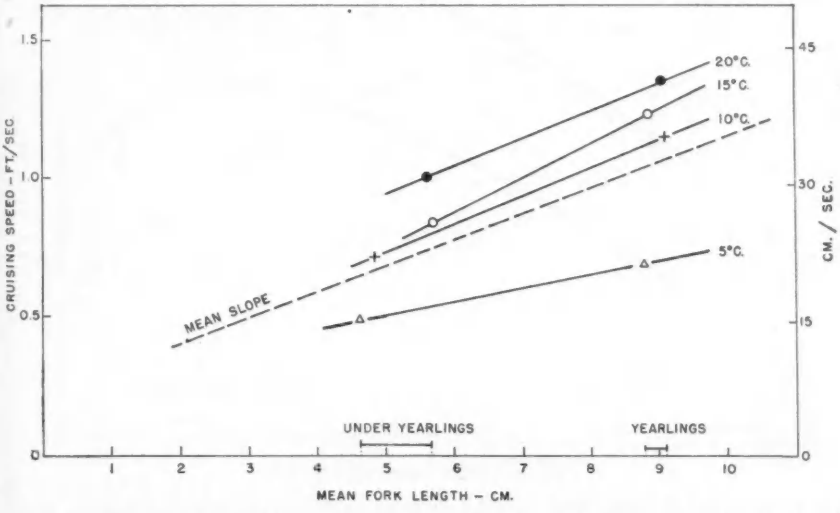

FIG. 5. Mean cruising speed for underyearling and yearling coho salmon, for four levels of acclimation. In general, from the mean slope, for every increase in length of 1 cm. the cruising speed increased by about 0.09 ft. per sec. (3 cm./sec.).

slopes for different acclimations which would be of interest to determine with greater accuracy by more extensive testing. Lacking sufficient data to substantiate the possibility of significant differences, the data have been pooled to determine an overall mean slope. This has been applied to adjust the swimming rates to conform to a common mean length for each of the underyearling and yearling samples, leaving temperature and individual variability as the main sources of difference. In the case of coho the average increase in swimming speed for an increase in length of 1 cm. was approximately 0.09 ft. per sec. (3 cm./sec.); that for the sockeye was 0.07 ft. per sec. (2 cm./sec.).

Effect of Temperature

Peaks of sustained performance for *coho* occurred in the vicinity of 20°C., for both underyearlings and yearlings (Fig. 6). By slight extrapolation to determine the minimum rate, near 0°C., the maximum rate can be seen to be about 3 to 4 times that of the minimum. In the case of underyearlings with a mean fork length of 5.4 cm., the maximum was 1.0 ft. per sec. (30 cm./sec.) and minimum about 0.2 ft. per sec. (6 cm./sec.); for yearlings with a mean fork length of 8.9 cm. the maximum and minimum were 1.4 and 0.5 ft. per sec. (43 and 15 cm./sec.) respectively.

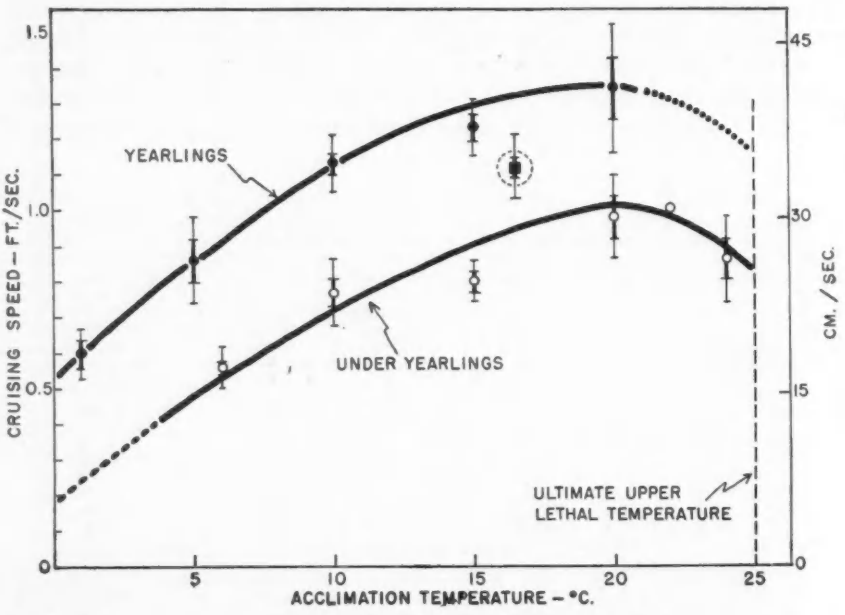

Fig. 6. Variation in cruising speed for temperature acclimated underyearling and yearling coho, adjusted in each age group to common mean lengths of 5.4 cm. and 8.9 cm. respectively. The circled point between two curves is for *exercised* underyearling coho acclimated to 16.5°C. (see text). Standard deviation and standard error are indicated for each sample.

The optimum temperature for performance in *sockeye* underyearlings occurred at about 15°C., which was 5°C. lower than that for coho (Fig. 7). A similar optimum is suggested from the limited data for sockeye *yearlings* (Table III). The maximum cruising speed for sockeye was also nearly three times the minimum level, providing swimming speeds of the following order for underyearlings (mean fork length 6.9 cm.): maximum 1.1 ft. per sec. (35 cm./sec.), minimum 0.4 ft. per sec. (12 cm./sec.).

Effect of Exercise

The group of coho which were placed in the circular culture tank, and were free to swim at a velocity up to 0.8 ft. per sec. (24 cm./sec.), showed quite significant differences in their ability to perform (Table IV). Not only did they display a higher cruising speed but also showed greater endurance at the elevated level. In Figure 6 the adjusted rate is plotted for comparison with underyearlings of equal size. The mean rate for exercised fish falls midway between the unexercised underyearling and yearling cruising speeds. As a direct comparison a sample taken from the same stock, but held in a standard trough, showed a high tendency to fatigue (3 out of 4) within the first hour. A cruising speed, as defined, could not be determined. The mean *peak* rate of the unexercised coho was 0.86 ft. per

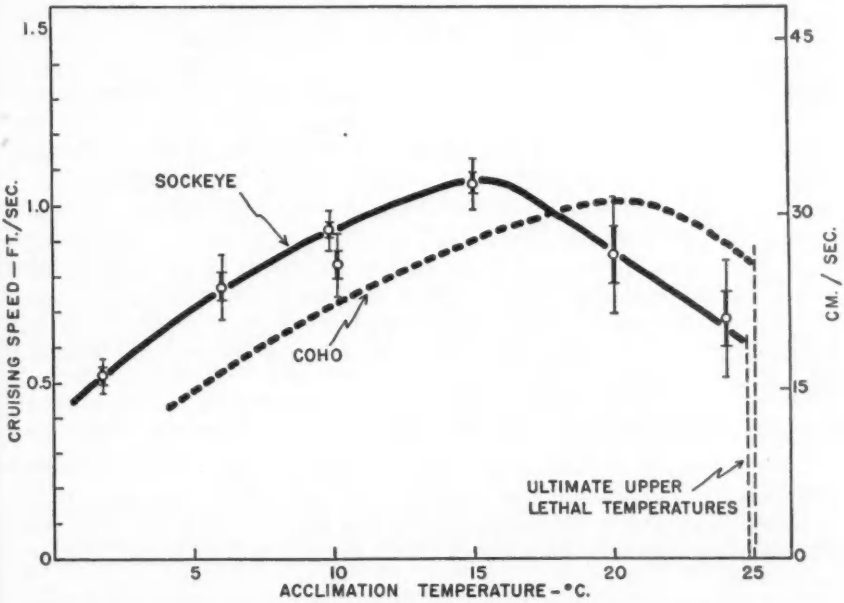

Fig. 7. Variation in cruising speed for temperature acclimated underyearling sockeye and coho, adjusted in each case to common mean lengths of 6.9 cm. and 5.4 cm. respectively. The samples were cultured under similar conditions and are of comparable age, 4 to 6 months from hatching. (The curve for coho is the lower curve of Figure 6.)

TABLE IV. Effect of exercise on the cruising speed of coho underyearlings. A control or unexercised sample showed a high incidence of early fatigue which did not permit an estimate of the cruising speed. The figures entered for this sample are for the maximum speed maintained for 5 minutes during the 30–40 minute test period, prior to the onset of fatigue. Speeds have been adjusted to the equivalent for coho of mean fork-length 5.45 cm. (Table II).

Acclimation temperature	No. fish	Mean length	Mean weight	Mean speed	S.D.	S.E.	Adjusted speed	
°C.		*cm.*	*g.*	*ft./sec.*	*ft./sec.*	*ft./sec.*	*ft./sec.*	*cm./sec.*
Exercised								
16.5	8	6.71	3.58	1.22	0.09	0.03	1.10	33.6
Unexercised								
16.5	4	6.53	3.28	0.87	0.19	0.09	0.77	25.4

sec. (26 cm./sec.), which was significantly below the mean cruising speed of 1.22 ft. per sec. (37 cm./sec.) for the exercised sample (Table IV).

DISCUSSION

The locomotion of fishes has been studied in particular by Denil (1938) and Gray (1953, 1957). Attention was directed mainly to the mechanics of movement in water, the force of propulsion developed by the caudal fin, and the maximum speeds attained. In general, there are relatively few records of the speed at which fish can swim, either as a maximum burst or as a sustained effort.

Until the work of Fry and associates (Fry, 1947; Fry and Hart, 1948; Graham, 1949; Gibson and Fry, 1953) few systematic studies on the effect of temperature on the swimming ability had been conducted. Elson's earlier work (Elson, 1939, 1942; Fisher and Elson, 1950) and that of Rogers (see Fry and Hart, 1948) concerning the effect of temperature on general activity and swimming rate of speckled trout (*Salvelinus fontinalis*) pointed to the existence of temperature optima. Fry (*loc. cit.*) was able to relate optimum performance to the maximum *scope for activity* by comparing the difference between active and standard metabolism with the cruising speed; when tested over a wide range of acclimation temperatures the greatest difference in metabolic rates correspnded with the maximum sustained cruising speed for a variety of species (goldfish, bullhead, speckled trout, lake trout).

SWIMMING PERFORMANCE

The technique of stimulating a fish to swim in a rotating annular trough permits an examination of the progressive changes which take place in the sustained effort. This would not be possible in a fixed unit such as a flume with moving water since temporary slumps would result in forcing the fish against a back screen.

The phases in performance illustrated in Figure 4 provide a pattern comparable in many ways with the performance of a long-distance runner. The initial period of bursts of activity is limited, and apparently over-taxes the respiratory system, resulting in a slump, probably reflecting a slight oxygen debt. It may also

be accompanied at this stage by an increase in lactic acid as Black (1955, 1957a,b,c) has demonstrated from experiments employing severe exercise. However, since there is recovery lasting for one or more hours, the initial severity is not of lasting consequence. The cruising period shows an oscillation about the mean rate with crests appearing about 20 minutes apart, but varying between 15 and 25 minutes. This reflects the basic mechanism of homoeostasis which does not signify a true steady state, but rather a continual return to a mean level, involving oscillations of relatively small magnitude. The onset of fatigue was often characterized by an increase in the extent of the oscillation, sometimes returning to a series of bursts followed by temporary slumps, then complete collapse. In collapse the fish turns over, respiring deeply, makes no muscular effort and is almost completely lacking in response to a strong stimulus, such as that produced by pinching the caudal peduncle with forceps. Since each fish was subsequently killed for weight–length measurements, no follow-up in cases involving fatigue or collapse was made. In view of Black's (*loc. cit.*) recent work this would be of interest in future studies.

The occurrence of fatigue and the general low level of performance in cultured fish is also of interest in relation to the findings of Miller (1952, 1954, 1958) and the problem of survival of hatchery-reared trout in streams. Miller (1952) reported that a third of the 3-year-old and half of the 2-year-old cutthroat trout (*Salmo clarki*) died, mainly in the first two weeks, following planting in a small mountain stream. All the cultured fish lost weight for 40 days, apparently through inability to compete with the native population. Miller (*loc. cit.*) further concluded that the trout probably drifted downstream after planting and that mortality was due to exhaustion, accompanied by acidosis or starvation.

In view of the large benefit obtained in young coho from exercise, eliminating early fatigue, there would seem to be some explanation provided by these experimental results and a possible remedy provided for the problem of fatigue in hatchery-reared trout after release.

There is another problem in which exercise may prove to be of significance. Phillips and associates at the Cortland hatchery, New York, (Phillips and Balzer, 1957; Phillips *et al.*, 1957) have pointed up the difference in chemical balance of the body constituents in wild and cultured fish despite the great attention given to the nutritional components of the diet. It would be profitable to determine how exercise affects the balance of protein and fat in the musculature and other tissues of cultured fish.

Swimming Rate

Turning to the matter of the actual level of swimming rate, it is apparent that if approach velocities above dams exceed 1.0 ft. per sec. (30 cm./sec.) a real problem for safe-guarding underyearlings is presented. Their capacity to stem such a current for more than an hour is limited to a relatively small temperature range, 12.5–17.5°C. for sockeye, and 18.5–21.5°C. for coho. In the case of sockeye, which usually migrate as yearling fish, the above range of temperature would apply for an approach velocity of approximately 1.4 ft. per sec. (43 cm./sec.).

The case for exercised fish might elevate these velocities provided that lake residence, in the case of young sockeye, results in an equivalent exercised condition. It may well be that the high selection in nature (1% to 3% survival to migration in sockeye–Foerster, 1938; Brett, 1948) could result in a wild stock better capable of performing than the unselected cultured fish.

Kerr (1953), in velocity studies on wild young spring salmon (*O. tshawytscha*) of average length between 3 and 5 cm., found their swimming capacity to range from 1 to 1.5 ft. per sec. (30–45 cm./sec.) for 10 minutes endurance in a test flume. When exposed for an hour or more, only velocities of the order of 1 to 1.2 ft. per sec. (30–37 cm./sec.) could be endured. No record of the temperature at which these tests were conducted is included. The swimming speeds are approximately the same as those for 20°C. acclimated underyearling coho.

The maximum observed speeds of fish tabulated by Gray (1953, 1957) constitute records of burst performances. They cannot be compared with sustained cruising speeds, which appear to be about one-quarter the velocity of the former. Field observations on migrating yearling sockeye and coho (mean lengths 9.4 and 10.1 cm., temperature 12–15°C.) indicate that velocities of 4.5–5.0 ft. per sec. (140–150 cm./sec.) represent maximum exertions. It must be emphasized that the ability of young salmon to swim rapidly is a very short term one. Sustained speeds are restricted to relatively low velocities, even as low as 0.5 ft. per sec. (15 cm./sec.) when the temperature is down to 5°C.

Temperature-Performance Relations

Although sockeye and coho juveniles inhabit the same lakes and migrate through the same rivers, where the territories of these two species can be said to really overlap, there are significant differences both in the areas selected and in the general behaviour during freshwater residence. During the summer in central and southern British Columbia lakes, underyearling sockeye are limnetic, frequenting the open water and subsurface regions. They feed in a zone centering around the 10 foot (3 m.) level and move in schools as a drifting mass coming up to the surface only in the evening (W. E. Johnson, personal communication). Seaward migration occurs in the spring of the year shortly after the ice has left more northern lakes, or following rising spring temperatures in southern lakes which may remain open throughout the year (Foerster, 1937). Termination of the migration is correlated with increasing surface temperatures, above about 12–14°C. High temperatures appear to be avoided. Protection is sought in the midst of the school and away from the competitive shallows where coho and minnows such as the shiner, *Richardsonius balteatus*, abound.

Johnson (1956) in many sampling hauls in the open waters of British Columbia lakes has never caught a single coho, yet they can be found readily during the summer in small streams, in the outlet rivers of lakes, and along the shores in shallow bays. They actively defend territory (Hoar, 1951) and forage for food with vigorous intraspecific competition, quite unlike schooling young sockeye. Although a segment of a coho population migrates seaward as yearlings in association with sockeye, coho continue to move after sockeye have ceased to

migrate, despite elevated temperatures. Their whole behaviour shows them to be capable of meeting the demands of increased metabolism and active competition in considerably warmer waters than is characteristic of sockeye.

These major ecological differences are only slightly if at all reflected by temperature tolerance differences. The cruising speed measures, however, reveal basic differences in performance which provide strong evidence for distinguishing the species on grounds of *temperature-dependent activities*. The pronounced peak performance in sockeye at 15°C. contrasts with the broader optimum for coho at 20°C. (Fig. 7). The greater scope for activity exhibited by sockeye at low temperatures lends further emphasis to the distinction. It can be predicted that the active metabolic curves for these two species will follow much the same pattern as the performance curves (cf. Fry, 1947).

Instead of abandoning temperature as an environmental identity strongly affecting the difference in distribution of these two species, it would appear that it may well have been the basic divergent factor from which other behaviour characteristics have evolved. Zoogeographic studies should place as much emphasis on *temperature-performance relations* as on *temperature-tolerance limits*.

Areas of Equal Activity

The role of temperature as an environmental factor affecting activity and survival was demonstrated by Fry (1947) to fall in two categories: either as a *governing* factor setting the pace of metabolism and hence the scope for activity, or as a *lethal* factor destroying life. The manner in which temperature governs the maximum activity in sockeye and coho has been described. In considering how environmental factors can cause stress in organisms, Brett (1958) further classified temperature as an *inhibiting* factor which, at low levels, could depress metabolism to the point of near or total inactivation, or could so *load* basal metabolism at high levels that activity is seriously curtailed. Figure 8 illustrates the various kinds and levels of temperature influence for young sockeye. The combination of two demands on performance, that of swimming at 0.5 ft. per sec. and that of meeting a metabolic load of equivalent energy demand, restricts the thermal zone in which these can be met to between 13.5° and 17.5°C.

The examination of lethal temperatures led Fry *et al.* (1942) to propose a zone of thermal tolerance, bounded by upper and lower lethal limits. Using a criterion of activity, namely capacity for growth, another zone could be defined bounded by the temperatures which permit such basic activities as growth to occur. Donaldson and Foster (1941) discovered that growth in young sockeye tends to be poor to none-at-all at temperatures above 21°C. and below 4°C. Using these temperature limits an area or "zone of adequate activity" has been constructed in Figure 9. A corresponding activity zone has been determined for coho, by equating the levels of common activity, using equal swimming speeds. These two zones are shown, framed by the zone of tolerance for the two species. A single area for lethal limits is shown. Slight differences do exist (Brett, 1952) but, by comparison with the zones of adequate activity, the differences are not of the same order of magnitude.

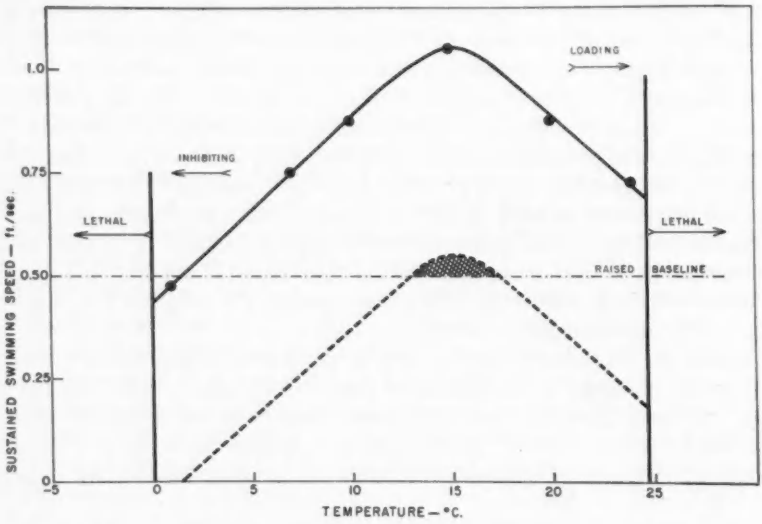

FIG. 8. Relation between performance and temperature for acclimated young sockeye. The dotted curve represents the remaining energy (capacity to swim) when stemming a current of 0.5 ft. per sec. (15 cm./sec.). The raised base-line has been elevated by an amount equal to the energy demand of swimming at 0.5 ft. per sec. and represents an assumed increment from imposed multiple stress. Only in the cross-hatched area could young salmon meet this situation. (From: Brett, 1958).

Although the determining of adequate activity zones may turn out to be impractical, it serves in this instance to show the highly significant difference in temperature relations that can exist within roughly the same framework of lethal levels. This sort of reasoning points up the need for a comparative study of such activities as swimming, growing, digesting and osmoregulating, in relation to temperature, to determine whether the measure of one activity reflects the level of another. Experiments by Fisher and Elson (1950) on the response of speckled trout to an electric stimulus suggest that there is a comparable level of optimum sensory response and optimum cruising speed (as determined by Graham, 1948) for speckled trout. If this can be shown to apply more generally, such a system of determining zones of adequate activity might prove useful.

SUMMARY AND CONCLUSIONS

The cruising speed has been defined as that rate which a fish can maintain for a minimum period of one hour under strong stimulus without gross variation in performance.

In a rotating trough, subjected to gradual acceleration, a period of swimming characterized by sudden bursts or darts preceded a period of slump, which was then followed by sustained performance. This latter, the cruising speed, is not

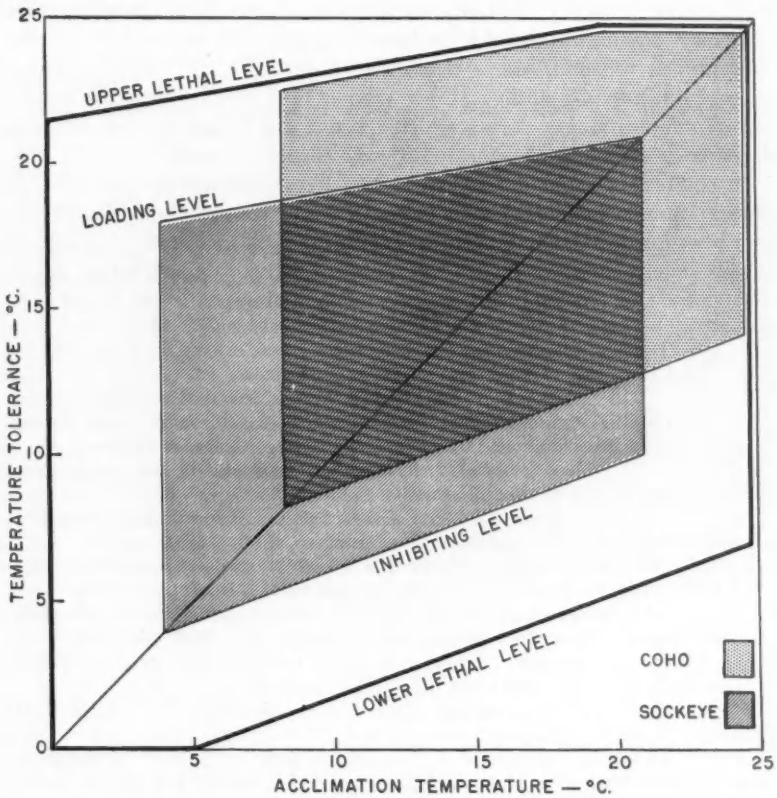

FIG. 9. Zones of temperature tolerance for young sockeye and coho salmon. Outer boundary represents a common lethal limit for both species. Inner zones represent areas in which the two can be equally active, as defined by the temperatures which permit equal cruising speeds for fish of the same age.

performed as a steady state but follows a pattern of small oscillations about a mean, the crests occurring approximately twenty minutes apart.

As has been reported by other investigators, temperature has a profound effect on the cruising speed. Underyearling coho (length 5.4 cm.) maintained a maximum rate of 1.0 ft. per sec. (30 cm./sec.) at an optimum temperature of 20°C., and were depressed to 0.2 ft. per sec. (6 cm./sec.) by a temperature approaching 0°C. By comparison, underyearling sockeye (6.9 cm.) of the same average age showed a maximum of 1.1 ft. per sec. (35 cm./sec.) at an optimum temperature of 16°C. and a minimum of approximately 0.4 ft. per sec. (12 cm./sec.).

Exercised young coho showed a significantly increased cruising speed and a lesser susceptibility to fatigue. This observation suggests the need for appropriate

techniques for exercising cultured fish prior to release. The losses from fatigue during early stream life might be reduced accordingly.

Approach velocities above dams which exceed 1.0 ft. per sec. will cause increased difficulty in guiding young salmon into safe by-passes if more than 20 to 30 minutes elapse during which the fish are forced to stem the current. Fatigue from exceeding the cruising speed is likely to occur.

In contrast to slight differences in lethal temperature, the profound differences in optimum temperature for performance of young coho and sockeye provide a basis for distinction of their different ecological niches in a common water mass. By determining the "zones for adequate activity" a method of displaying the magnitude of the temperature-performance difference is presented.

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The Preferred Temperature of Fish and their Midsummer Distribution in Temperate Lakes and Streams[1, 2]

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ABSTRACT

Laboratory studies of preferred temperature with yellow perch (*Perca flavescens*) are compared with results from 21 other species. These show that temperature, if acting alone, can determine the distribution of fish in laboratory apparatus. Factors such as light, conditioned responses related to feeding routines, and social behaviour can interfere with the expression of the response to temperature. Subdued lighting conditions were necessary in the experiments with *Oncorhynchus*, *Salvelinus* and *Coregonus*, whereas full daylight was required in experiments with *Perca flavescens*.

The level of thermal acclimation influences the range of temperature preferred. In general the preferred temperature is considerably higher than the acclimation temperature at low thermal acclimations, but this difference decreases up to the final preferendum, where both coincide. The final preferendum and the relation between acclimation and preferred temperature is characteristic for the species. The shape of the resulting curve may have some value in interpreting observations of fish mortalities and distribution in nature. The final preferendum of the yellow perch from the present work was 24.2°C., from other work using older fish it was 21.0°C.

Summer field observations of yellow perch in Lake Nipissing, Costello Lake and Opeongo Lake, in Ontario, showed average thermal distribution of 19.7°C., 21.0°C. and 21.2°C. respectively. This agrees well with 20.8°C. observed for four Wisconsin lakes. Oxygen depletion reported for Tennessee Valley reservoirs, distribution of primary prey species of lake trout in New York waters, and other factors, have been shown to modify the thermal distribution in nature. Differential sex response to temperature may be important in the perch. Field observations of thermal distributions for other species are also presented.

A comparison of the laboratory and field data shows good agreement with fish having colder final preferenda: *Salvelinus fontinalis*, *Salvelinus namaycush*, *Salvelinus* hybrid and *Coregonus clupeaformis*. Fish with warmer final preferenda, such as *Micropterus salmoides*, *Micropterus dolomieu* and *Lota lota lacustris*, showed higher temperatures in the laboratory than was shown by field observations. Young *Perca flavescens* showed similar results, but experiments with older perch showed excellent agreement between laboratory results and field observations. The lack of agreement between laboratory results and field observations is attributed to age differences; laboratory experiments being performed with young fish and field observations being made on older fish.

INTRODUCTION

It is my purpose to discuss the influence of temperature on fish distribution, drawing on laboratory evidence and field examples. The characteristic of animals to move into specific thermal conditions when a range of temperatures is available to them has been termed thermal preference or selection; here the term preference

[1]Received for publication February 19, 1958.

[2]A paper presented at the 11th Meeting of the Canadian Committee on Freshwater Fisheries Research, at Ottawa, January 3, 1958.

J. Fish. Res. Bd. Canada, 15(4), pp. 607–624, 1958.
Printed in Canada.

will be used. Fry (1947) has defined the preferred temperature as the "region, in an infinite range of temperature, at which a given population will congregate with more or less precision", and the final preferendum as "a temperature around which all individuals will ultimately congregate, regardless of their thermal experience before being placed in the gradient".

There have been two approaches taken to study the preferred temperatures of fish; the description of the mechanism, and the classification of the various species in terms of their response to temperature. We are concerned with the latter here.

The preferred temperature studies in the laboratory will be reviewed and some examples of field observations will be presented to help establish the relation of preferred temperature to midsummer distribution. Experiments in the laboratory with yellow perch (*Perca flavescens*) will provide the basis for the laboratory discussions. Analysis of Lake Nipissing yellow perch data from the records of the Ontario Fisheries Research Laboratory, and similar data from Lake Opeongo and Costello Lake made available through the kindness of Drs. R. R. Langford and W. R. Martin, will provide the basis for the discussion of the field examples.

LABORATORY STUDIES OF PREFERRED TEMPERATURE

General Laboratory Procedure

The test chamber used for the yellow perch experiments was a tank 36 by 20 by 36 inches (94 × 57 × 94 cm.) and utilized a vertical gradient (see Brett, 1952, for a photograph and description). This tank was used in most of the studies reported herewith. Test chambers utilizing horizontal gradients have been of various dimensions and construction (see Doudoroff, 1938; Fisher and Elson, 1950; Tompkins and Fraser, 1950; and Sullivan and Fisher, 1952). The thermal gradients employed in the various experiments have varied with the experiment and the acclimation level of the population; in general the gradients approximated 0.5°C. per inch (0.2° per cm.), and included the acclimation temperature. Nearly all the experiments have been conducted under subdued light, especially those involving salmonids or coregonids; the yellow perch were tested in full daylight, some workers employed cameras and synchronized lights for observations in total darkness.

In general the fish have been introduced from their acclimation tanks at least 24 hours, and fed at least 8 hours, previous to the experiment. The operators have taken special pains not to disturb the fish during the experiment; in some cases special baffles were constructed to screen the observer from the fish. The gradient has been recorded at the beginning and end of each experiment. The distribution of the fish in the various segments of the gradient has been observed, and replication of the observations made to obtain sufficient data for reliability. Generally there have been consecutive series of experiments for each acclimation, with alterations in the gradient throughout the series, and a number of control observations without any gradient.

Limitations in Laboratory Studies

Laboratory studies of preferred temperatures have some limitations which must be taken into account if their value is to be properly judged. Space and possibly time limitations in the laboratory are probably the most important deviations from natural conditions. Space limitations result in more interference from physical boundaries, more contact with other individuals, and compressed thermal gradients. Space and other considerations limit the number of individuals and the size of the individuals to the extent that most laboratory studies are of fish in the fry or fingerling stage. Fish behaviour under laboratory conditions must also be taken into account in the analysis; territorial behaviour and peck-order were observed in the experiments of Pearson (1952) with hybrid *Salvelinus* and some schooling was observed in the experiments with yellow perch. Conditioned responses related to laboratory feeding procedures were also mentioned by Brett (1952) for *Oncorhynchus* and by Pearson (1952) for *Salvelinus* hybrids. Yellow perch (*Perca flavescens*) were inactive in the dark and settled to the bottom, whereas speckled trout (Sullivan and Fisher, 1954; Graham, 1948), *Salvelinus* hybrids (Pearson, 1952), *Oncorhynchus* (Brett, 1952) and *Coregonus* (Tompkins and Fraser, 1950) were more precise in their temperature responses in subdued light.

Vertical and Horizontal Gradients

Both vertical (Brett, 1952; and others) and horizontal (Doudoroff, 1938; Tompkins and Fraser, 1950; Sullivan and Fisher, 1953) thermal gradients have been employed in laboratory experiments to determine thermal preferenda. The former presumably simulate thermal gradients as they occur in lakes, and the latter, stream conditions. A tactile factor would appear to be a major consideration when dealing with fish that normally keep contact with the bottom in their natural habitat.

Experiments on yellow perch are described below to illustrate the laboratory procedure and results.

Preferred Temperature of the Yellow Perch

The apparatus and procedure as described by Brett (1952) were found suitable for experiments with the yellow perch (*Perca flavescens*), with slight modifications. All experiments were conducted in light corresponding to conditions in a well-lighted room. Modification of the observation technique (observation of one level at a time and replication through all levels) was made necessary by the rapid swimming activity of the perch when a thermal gradient was introduced. This rapid swimming throughout the experimental tank decreased if the fish remained three to four hours in the thermal gradient. In general initial observations were made three hours after the initiation of the gradient; subsequent observations were made approximately one hour apart.

The vertical distributions of a sample of yellow perch acclimated to 15°C. are shown for various thermal gradients in Figure 1. It is clear that these fish

were more often associated with the thermal conditions in the 20–25°C. range than any other physical feature of their environment; with alteration in the depth of these thermal conditions there was a corresponding shift in the distribution of the fish.

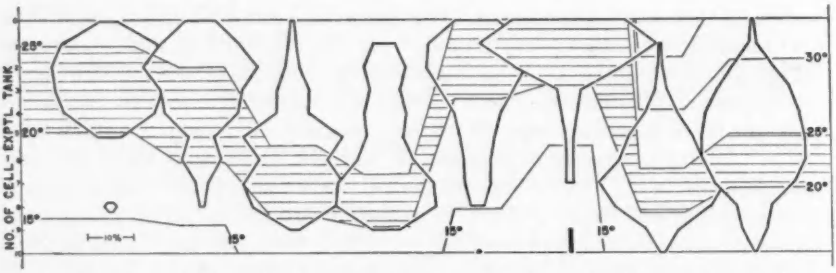

FIG. 1. The vertical distribution of yellow perch (*Perca flavescens*) and temperature isotherms (°C.) in a laboratory experiment. The distribution of fish is expressed as a percentage in each cell. Fish were acclimated to 15°C. Time between observations was approximately one hour, with two to three hours initially between start of gradient and first observation.

This figure also serves to illustrate a number of other points about laboratory preferred temperature experiments. Refractory individuals (see 1st, 5th and 6th distribution, Fig. 1) which did not respond to the gradient and remained near the bottom, and the effects of limited space (6th distribution, Fig. 1) where the fish were crowded into the upper strata by thermal conditions, were not included in the calculation of the mean temperature distribution. It should also be noted (7th distribution, Fig. 1) that yellow perch will continue to invade temperatures in excess of their upper lethal temperature (29.7°C. in winter, 32.3° in summer: Hart, 1952) and if the experiment is prolonged under these conditions the fish accumulate a lethal dose.

The preferred temperatures of the yellow perch at six different acclimations are shown in Table I; these results are compared with the unpublished results of

TABLE I. The mean or modal preferred temperature of the yellow perch at different acclimation temperatures. A—present experiments; B—McCracken and Starkman (1948). All temperatures are in degrees Centigrade.

Acclimation temperature	Preferred temperature A		B
	Mean	Mode	Mode
5	...	...	11.0
8	18.6	(17.5)	...
10	19.3	(20.6)	17.0
15	23.0	(24.5)	20.0
20	23.1	(21.5)	20.5
25	24.5	(24.0)	21.5
30	26.7	(26.5)	27.5
Final preferendum	24.2	...	21.0
Number of fish	10–12		3–4
Age of fish	fingerling		2 yrs. old or older
Experimental period	Apr., May, Aug.		Feb., Mar.

McCracken and Starkman (1948). It will be noted that although the apparatus and routine were similar, there were differences in the numbers of fish tested, the size of fish, and the season of experimentation. Any one of these factors could account for the discrepancy in the results of the two sets of experiments. Age may have a significant effect here, as it did with the cisco as shown by Fry (1937) in field studies. The season of experimentation may also have influenced the results as was shown for the speckled trout by Sullivan and Fisher (1952).

Comparison of Laboratory Results

The relation between preferred and acclimation temperatures for the present data in comparison with selected published results are shown in Figure 2. The line at 45° represents all points where the acclimation temperature coincides with the preferred temperature. The point at which the preferred temperature crosses this line is the final preferendum. The species presented were chosen to show the range of the temperatures preferred by fish, and the relation between the acclimation and preferred temperatures.

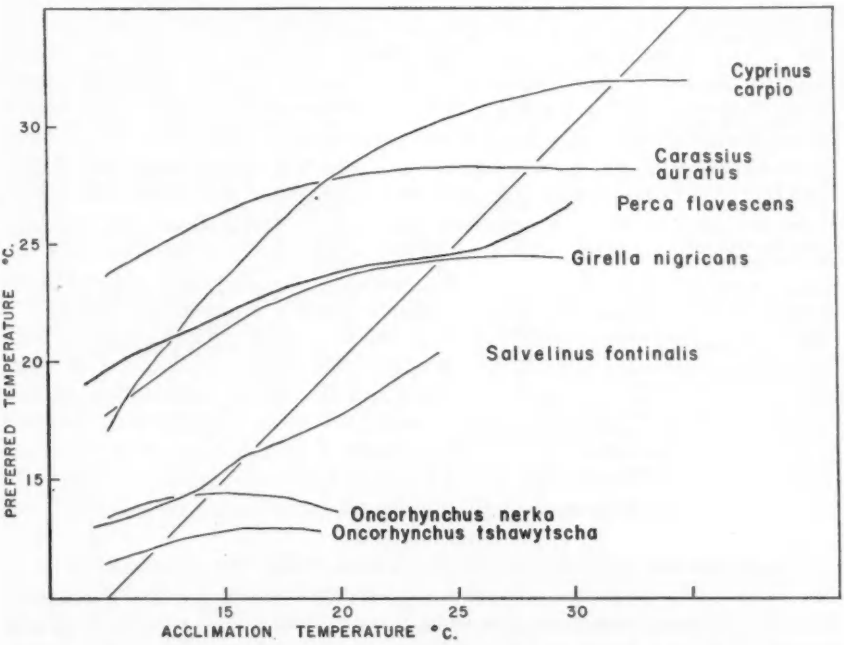

Fig. 2. Laboratory studies of preferred temperature: the yellow perch (*Perca flavescens*) compared with various other fish. The line at 45° joins all points where preferred and acclimation temperatures coincide. Data from various sources: *Cyprinus*–Pitt, Garside and Hepburn (1956); *Carassius*–Fry (1947); *Girella*–Doudoroff (1938); *Salvelinus*–Graham (1948); *Oncorhynchus*–Brett (1952).

There has been a gradual accumulation of information on the preferred temperatures of various fish, mostly at the University of Toronto; some of which have been published, but many are manuscripts in preparation. Table II presents the final preferenda for a number of species for which data are available. These results are self-explanatory in most cases with the exception of the three instances where a range of temperature is shown rather than a single point. The preferred temperature curves for *Micropterus salmoides* and *Salvelinus fontinalis* tended to follow the preferred-acclimation line closely over this range. The results for *Salmo trutta* represent the range of preferred temperatures for fish living continuously in a thermal gradient for a period of two years. Tait (MS), whose work this is, considers the study preliminary at this stage and the manuscript is in preparation at the moment.

TABLE II. The final temperature preferenda for various species of fish as determined by laboratory experiments, in degrees Centigrade. Young of the year or yearling fish were used, except as noted.

Species	Final preferendum	Authority
Lepomis macrochirus	32.3	Fry and Pearson (MS, 1952)
Micropterus salmoides	30.0–32.0	Fry (MS, 1950)
Cyprinus carpio	32.0	Pitt, Garside and Hepburn (1956)
Lepomis gibbosus	31.5	Anderson (MS, 1951)
Carassius auratus	28.1	Fry (1947)
Micropterus dolomieu	28.0	Fry (MS, 1950)
Esox vermiculatus	26.0	Berst and Lapworth (MS, 1950)
Perca flavescens	24.2	Present work
Esox masquinongy	24.0	Jackson and Price (MS, 1949)
Girella nigricans[a]	23.5	Doudoroff (1938)
Lota lota lacustris	21.2	Crossman, Irizawa and Peacock (MS, 1953)
Perca flavescens	21.0	McCracken and Starkman (MS, 1948)
Salmo trutta[b]	12.4–17.6	Tait (MS, 1958)
Salvelinus fontinalis	14.0–16.0	Graham (1948); Fisher and Elson (1950)
Oncorhynchus nerka	14.5	Brett (1951)
Oncorhynchus keta	14.1	Brett (1951)
Salmo gairdnerii	13.6	Garside and Tait (MS, 1958)
Coregonus clupeaformis[c]	12.7	Tompkins and Fraser (MS, 1950)
Salvelinus hybrid[d]	12.0	Pearson (MS, 1952)
Salvelinus namaycush	12.0	McCauley and Tait (MS, 1956)
Oncorhynchus tshawytscha	11.7	Brett (1951)
Oncorhynchus gorbuscha	11.7	Brett (1951)

[a] *Girella*—a marine species.
[b] *Salmo trutta*—two years old or older.
[c] *Coregonus*—two-year-olds.
[d] *fontinalis* × *namaycush*.

FIELD OBSERVATIONS OF FISH DISTRIBUTION WITH ASSOCIATED TEMPERATURES

There are few field studies directly concerned with distribution of fish and the influence of temperature. The following data derived from published material, was in nearly every case from papers not concerned with thermal conditions and fish distributions *per se*. In order to derive thermal distribution from these papers it was necessary to take some liberties with the authors' data. In many cases the author's presentation did not lend itself to the derivation of average distributions and associated average temperatures at the pertinent depths; in these instances a range of temperatures was extracted.

Limitations in Field Studies

The study of the influence of temperature on field distributions of fish has limitations other than those found for laboratory studies. Some of these are inherent, and may not be adequately accounted for in the treatment of the data. These limitations include problems in capture where it is difficult to randomly and completely search all portions of the environment with equal intensity. Possibly the most serious limitation is in the collection and analysis of associated pertinent data and observations. Indeed, it is difficult to assess the multitude of factors posed. In the present analysis factors other than temperature will be ignored unless their influence is definitely suggested.

Yellow Perch Field Distribution and Thermal Preference

Netting studies in Lake Nipissing and routine limnological observations including a special cisco study (Fry, 1937), combined extensive netting with complete temperature records. This netting revealed the following seasonal distribution for perch. During the first half of May, before the warm-up period, perch were netted in small numbers from 60 to 150 feet (18–46 m.). In late May and early June perch were caught in small numbers from 20 to 30 feet (6–9 m.), but there was not adequate netting in deeper water. During the period of thermal stratification perch were only netted in the epilimnion, and in the vicinity of the 20° isotherm; they tended to move from their shallow distribution in mid-June to follow the 20° isotherm to its greatest depth in early August. In late August and early September there was not adequate netting in water less than 30 feet deep, but the indications are that perch were not present in numbers deeper than 30 feet. Netting in the fall did not allow assessment of their distribution. The same seasonal distribution for the European perch (*Perca fluviatilis*) was demonstrated by Worthington (1950) and Allen (1935) in Lake Windermere, but they did not present temperature data.

Records of intensive netting studies in two different lakes in Algonquin Park, Ontario, are available, coupled with extensive temperature data. They show the same summer perch distribution as was found in Lake Nipissing, but in sharper detail. The results of this work are presented in Figure 3A. The thermocline is similarly constituted in both these lakes with Costello tending to have a steeper gradient, and because of its sheltered nature, a shallower one. The top of the thermocline in both lakes closely corresponds to the position of the 20° isotherm. In neither of these lakes were oxygen conditions poor in the hypolimnion.

Netting studies of hybrid trout (*Salvelinus fontinalis* × *namaycush*) by Martin and Baldwin (1958) are shown in conjunction with the thermal conditions in Figure 3B and 3C. In these two Algonquin Park lakes thermal stratification varied considerably in depth and constitution in the different years, but the thermal position of the hybrid trout remained similar.

Fry's (1937) work on the cisco (*Leucichthys artedi*) is the most thorough treatment of field distribution of a fish that has come to our attention. He concludes that temperature is the principal factor influencing the vertical migrations

of these fish. He further demonstrates that age plays an important role in this fish's reaction to temperature. Figure 4 is a reproduction of Fry's figure showing

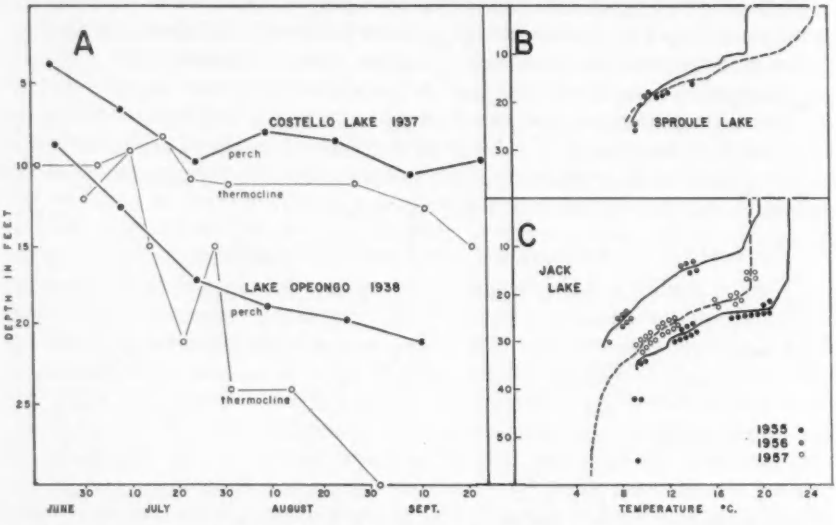

FIG. 3. *Panel A.* Mean distribution of yellow perch in relation to the top of the thermocline. Solid dots—perch mean depth; open dots—top of the thermocline.
Panels B and C. Depth distribution of hybrid trout (*Salvelinus fontinalis* × *namaycush*) in relation to thermal conditions. Each dot represents one fish. (Adapted from Martin and Baldwin, 1958.)

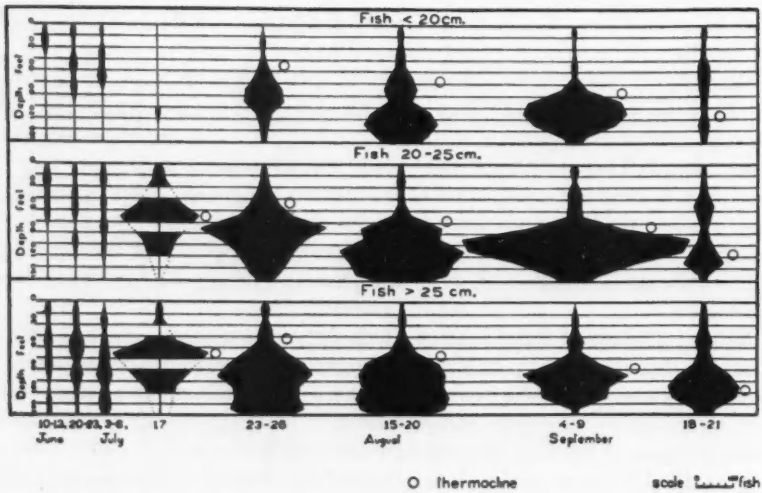

FIG. 4. Seasonal changes in vertical distribution in ciscoes of different lengths at station 4, Lake Nipissing, Ontario, 1935. (A reproduction of figure 15 of Fry, 1937, with the author's permission.)

the relative depth distributions of three different size groups of cisco and the relation of the thermocline to the distributions. In essence the younger fish remained longer in the upper, warmer water during the warm-up period; the return to the epilimnion in the fall was more complicated.

Dendy (1948) concluded from his work in three Tennessee reservoirs that accurate prediction of fish depth distribution could be made on the basis of knowing the thermal structure, due allowance being made for unfavourable oxygen conditions. Dendy's figure showing the thermal distributions of largemouth bass (*Micropterus salmoides*), walleye (*Stizostedion vitreum*) and sauger (*Stizostedion canadense*) is reproduced in Figure 5. This figure clearly demonstrates how these three species continue to increase their thermal experience up to a certain point, then each "levels off" at a particular thermal level, and does not radically depart from it unless that temperature stratum becomes deficient in oxygen.

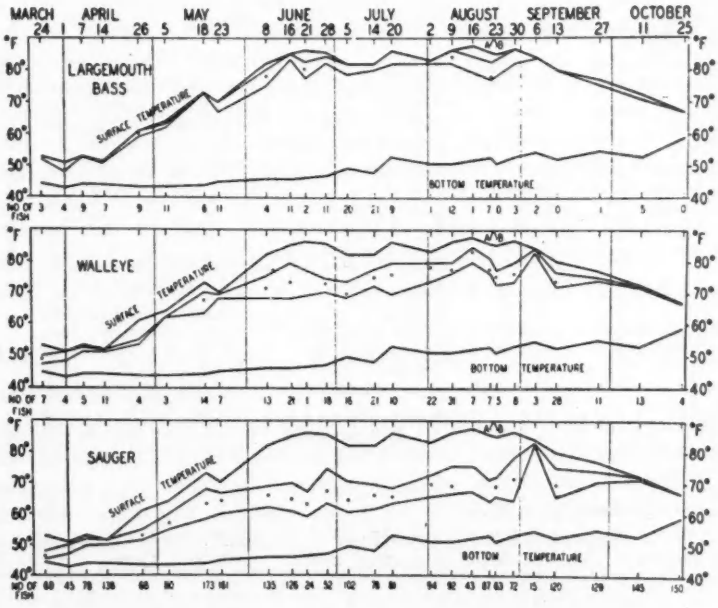

FIG. 5. Distribution of the middle 50% of largemouth bass, walleye, and sauger in relation to temperature, Norris Reservoir, 1943. The two middle lines show that temperature range of the middle 50% of the fish caught. When the range was wide, the temperature where the median fish was caught is indicated by dot. Presence of walleye in unusually warm water on August 16 and September 6, and of sauger in the same zone on September 6, resulted from oxygen shortages in the strata formerly occupied by these species. For further explanation see Dendy (1945, fig. 13, p. 128). (A reproduction of figure 2 of Dendy, 1948, with the permission of the author and the American Fisheries Society.)

The depth distribution of lake trout (*Salvelinus namaycush*) in Algonquin Park lakes (Martin, 1952) and in Cayuga Lake (Galligan, 1951) are in close agreement in the temperatures where these fish are located during the summer. Galligan (1951) makes the interesting observation that the July distribution of the lake trout was in much shallower water than would be expected, and this observation was correlated with the occurrence of alewives in shallow water during their spawning season.

The results presented above are summarized in terms of temperature in Table III. In addition to the above results, additional observations are included

TABLE III. Field observations of various species of fish and associated temperatures. Some temperatures are estimates derived from the author's tabled or figured data. August distributions and temperatures were used wherever possible.

Species	Temp., °C.	Water	Location	Author
Micropterus salmoides	26.6–27.7	Norris Reservoir	Tenn.	Dendy, 1948
Micropterus punctatus	23.5–24.4	,,	,,	,,
Stizostedion v. vitreum	20.6	Trout Lake	Wis.	Hile & Juday, 1941
,,	22.7–23.2	Norris Reservoir	Tenn.	Dendy, 1948
Dorosoma cepedianum	22.5–23.0	,,	,,	,,
Aplodinotus grunniens	21.6–22.2	,,	,,	,,
Ambloplites rupestris	14.7–21.3	Lakes	Wis.	Hile & Juday, 1941
,,	20.7	Streams	S. Ont.	Hallam, 1958
Perca flavescens	21.2	Lake Opeongo	Ontario	Present work
,,	21.0	Costello Lake	,,	,,
Perca flavescens (small)	12.2	Muskellunge Lake	Wis.	Hile & Juday, 1941
Perca flavescens (larger)	20.2	,,	,,	,,
Perca flavescens	20.2	Silver Lake	,,	,,
,,	21.0	Nebish Lake	,,	,,
,,	20.8	Trout Lake	,,	,,
,,	19.7	Lake Nipissing	Ontario	Present work
Micropterus dolomieu	20.3–21.3	Nebish Lake	Wis.	Hile & Juday, 1941
,,	21.4	Streams	S. Ont.	Hallam, 1958
Stizostedion canadense	18.6–19.2	Norris Reservoir	Tenn.	Dendy, 1948
Salvelinus fontinalis	14.2–20.3	Moosehead Lake	Maine	Cooper & Fuller, 1945
,,	15.7	Streams	S. Ont.	Hallam, 1958
,,	12.0–20.0	Redrock Lake	Ontario	Baldwin, 1948
Cottus bairdii	16.5	Streams	S. Ont.	Hallam, 1958
Salvelinus hybrid[a]	13.1	Jack L., Sproule L.	Ontario	Martin & Baldwin, 1958
Catostomus commersonnii	11.8–20.6	Musk., Trout, Silver L.	Wis.	Hile & Juday, 1941
Catostomus c. commersonnii	14.1–18.3	Moosehead Lake	Maine	Cooper & Fuller, 1945
Prosopium cylindraceum	13.9–17.5	,,	,,	,,
Pomolobus pseudoharengus	4.4– 8.8	Cayuga Lake	N.Y.	Galligan, 1951
Salmo salar sebago	13.6–16.2	Moosehead Lake	Maine	Cooper & Fuller, 1945
Salvelinus namaycush	10.0–15.5	Cayuga Lake	N.Y.	Galligan, 1951
,,	14.0	White Lake	Ontario	Kennedy, 1941
,,	11.0–11.5	Moosehead Lake	Maine	Cooper & Fuller, 1945
,,	8.0–10.0	Louisa, Redrock L.	Ontario	Martin, 1952
Osmerus mordax	12.8	Lake Champlain	N.Y.	Greene, 1930
,,	6.6– 8.3	Cayuga Lake	N.Y.	Galligan, 1951
Coregonus clupeaformis	11.4–11.9	Moosehead Lake	Maine	Cooper & Fuller, 1945
Catostomus catostomus	11.0–11.6	,,	,,	,,
Lota lota maculosa	10.8–11.4	,,	,,	,,
Leucichthys artedi	8.0–10.0	Lake Nipissing	Ontario	Fry, 1937
,,	5.5–7.2	Cayuga Lake	N.Y.	Galligan, 1951
Oncorhynchus nerka	10.6±0.44	Cultus Lake	B.C.	Foerster, 1937

[a] *fontinalis* × *namaycush*.

from other papers, the range or average temperature presented being subject to the limitations mentioned earlier. In each case the data were derived from depth distributions transposed to temperatures at this depth, from the author's tabled or figured data, with the following exceptions. In some cases the author derived and mentioned the temperature at the average depth distribution. The temperature for *Salvelinus namaycush* in White Lake (Kennedy, 1941) is the temperature of White Lake at the time of peak migration from this lake into a deeper lake. The temperature for *Oncorhynchus nerka* is the 8-year average temperature at the time of cessation of the downstream migration for this species (Foerster, 1937). The temperature for *Osmerus mordax* in Lake Champlain is the temperature recorded by Greene (1930) which is avoided by this species. These latter three examples, while admittedly different from the remainder, are close to the defined final preferendum. The temperatures recorded for stream fish by Hallam (1958) are average stream temperatures where these species were found.

Wherever possible August distributions and temperatures were used since these would best represent conditions where the maximum range of temperatures were available, and it also represents a period when spawning activities do not interfere with the behaviour of the fish.

Graphical presentation of the data in Table III allows easier appreciation of the thermal position of each of the species; this has been presented in Figure 6. Wherever information from several sources are available and overlapping, the range or average for the different waters are presented (except in the case of the perch where there is close agreement in all average temperatures). It should be emphasized that the range presented for the species does not necessarily represent the species' preferred temperature, but is primarily a function of the ease or difficulty experienced in handling the author's data.

DISCUSSION

Laboratory Studies

Laboratory studies are of value in the interpretation of field observations, but the limitations of each must be kept in mind. Laboratory results have clearly demonstrated that temperature acting alone can control the distribution of fish in laboratory apparatus. Aggregations of fish have been induced in specific temperature ranges in both horizontal gradients (Doudoroff, 1938; Sullivan and Fisher, 1953; Fisher and Elson, 1950; Sullivan and Fisher, 1952; and others) and vertical gradients (Fry, 1947; Brett, 1952; Pitt, Garside and Hepburn, 1956; and others). Various authors have found that light (Sullivan and Fisher, 1954; Brett, 1952; Pearson, 1952; and others), feeding activity (Brett, 1952; Pearson, 1952; and others), and social behaviour (Pearson, 1952) interfered with precise temperature selection in fish.

It has been demonstrated that thermal acclimation has a significant effect on the preferred temperature, by Fry (1947), Pitt, Garside and Hepburn (1956), and others. Doudoroff (1938) considered the influence of acclimation as temporary since *Girella*, when acclimated to 10°C., would always move into, and

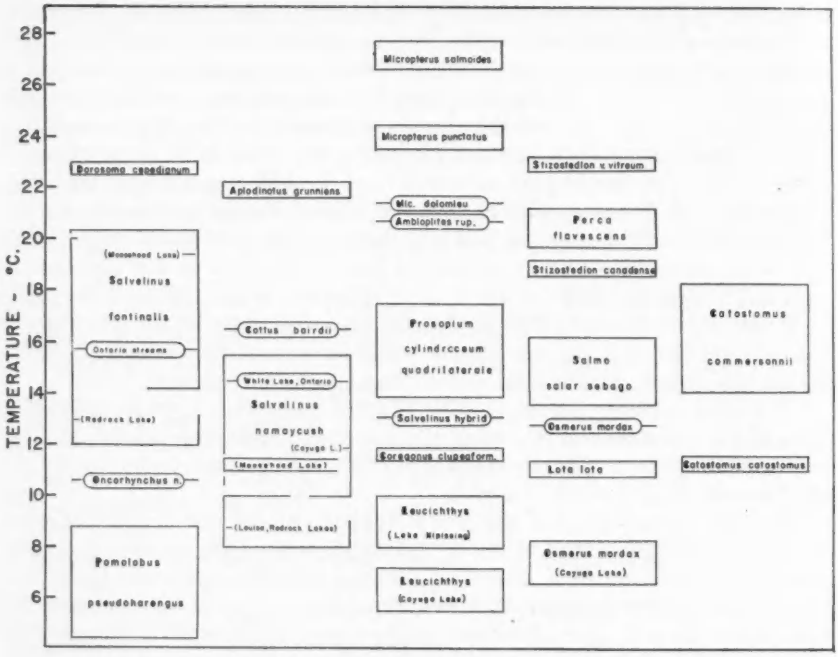

FIG. 6. Field observations of fish and associated temperatures during midsummer (August mostly). The depth of each rectangle corresponds to the temperature range. Pointers on laterally rounded figures represent a derived average. Vertical relations only are important. (Data from various sources; see also Table III.)

would eventually become acclimated to, higher temperatures. Doudoroff's conclusion is not in contradiction to the other studies, but serves to emphasize that laboratory studies illustrate specific points at various acclimation levels, a process that would be continuous in nature during spring and summer.

The final preferendum in the laboratory, as defined by Fry (1947), is that temperature where the temperature preference is the same as the acclimation level. In nature this would be manifest as the temperature where the fish would eventually congregate.

PREFERRED TEMPERATURE CURVES

Preferred temperature curves (Fig. 2) have not received detailed attention primarily because there have been too few for comparison. There appears a basic similarity in the portion representing acclimations lower than the final preferendum (to the left). Presumably this portion of the curve gives some indication of the relative rate at which a given species may move into progressively warmer water. Thus at low acclimation temperatures fish have a strong tendency for moving into warmer water. There are a number of recorded cases in the literature where fish acclimated to low temperatures invade warm water in large numbers

in spite of a lethal effect. These cases are recorded or noticed more readily because an extensive mortality ensues, likely because the temperatures are lethal for fish at low acclimation temperatures. Gizzard shad (*Dorosoma cepedianum*) from Lake Erie in the vicinity of the Port of Erie, Pennsylvania, during recent winters have moved into the warm water effluent of power plants where they die in large numbers (Hancock, 1954; and personal communication from A. Larsen). Alewives (*Pomolobus pseudoharengus*), according to Graham (1956), move into shallow warm water in late spring where they suffer extensive mortalities. Hancock (1954) also reports large aggregations of fish (mostly white crappie) in mid-winter in the presence of a local temperature gradient of 1–2 degrees.

Higher acclimations closer to the final preferendum presumably would be reflected in nature by a more gradual move into water at the temperature of the final preferendum. A comparison of the thermal experience of the surface waters and the perch in Lakes Nipissing, Opeongo and Costello would indicate this. The figure (Fig. 5) of Dendy (1948) also tends to show this, where two species experience the surface water warm-up until late spring, then sound to deeper water, but they then still increase their thermal experience at a slower rate. The largemouth bass which continually inhabited surface waters presumably might have invaded still warmer water had it been available.

Temperatures higher than the final preferendum would presumably move the fish out of surface waters. This would appear to be illustrated by the observations of Foerster (1937) who found young *Oncorhynchus nerka* left surface waters when the temperature rose to 10.6°C., and the observations of Kennedy (1941) who records *Salvelinus namaycush* moving into a cold lake from a warming lake when the latter reached 14°C.

Field Observations

One of the most decisive examples of the directive action of temperature in the field is reported by Hancock (1954). He showed that local large aggregations of fish (principally white crappie) were induced by a temperature gradient of 1–2°C. This was in the winter under ice cover.

Yellow perch

Yellow perch in Lake Nipissing were scattered throughout the lake to depths of 150 feet (46 m.) in the spring, but after the initial spring warm-up period they were only found in the surface waters, later, in mid- and late summer, they frequented the vicinity of the 20°C. isotherm. The Lake Opeongo and Costello Lake data show a similar distribution picture. This appears comparable with the yellow perch distribution in the Wisconsin lakes studied by Hile and Juday (1941). The average thermal distribution in August as derived from this paper was 20.8°C. Their record of smaller perch in deeper water (11 meters–12.2°C.) in Muskellunge Lake cannot be accounted for on present evidence. The differential depth distribution of the two sexes of perch reported by Eschmeyer (1938) may account for it. If this is the case, then sex should be considered in the thermal distribution of perch.

Worthington (1950) and Allen (1935) working with the European perch (*Perca fluviatilis*) in Lake Windermere, England, describe the same distribution as has been found for the yellow perch in Lakes Nipissing, Costello and Opeongo. Allen (1935) discusses this distribution and remarks on the coincidence of the distribution and thermal conditions, but does not credit temperature as being the factor triggering the movement into shallow water in the spring prior to spawning. He felt that sexual development must control this movement from deep water into shallow water. Neither author presented temperature data for Lake Windermere.

CISCO

Fry's (1937) study of the summer migration of the cisco is the most comprehensive treatment of the summer distribution of a fish, and of the causal factors, that has come to our attention. These fish move into shallow water in the spring and remain there for varying periods depending on their age and sex (Fig. 4). Fry related their movement from shallow water to deep water in late spring and early summer to rising temperatures in the epilimnion. They descended to the bottom in their initial sounding, but ascended to the lower thermocline in late summer. The decrease in oxygen and the increase in carbon dioxide in the bottom water was held responsible for concentrating the cisco below the thermocline. Fry considered the late summer piercing of the thermocline, and return to the epilimnion to be the resultant of the balance of intolerance to carbon dioxide and to high temperatures.

OTHER SPECIES OF FISH

Dendy (1946, 1948) has presented evidence in detail related to the thermal distributions of fish in various Tennessee Valley reservoirs. He also recorded the influence of dissolved oxygen on these distributions. Figure 5 is a reproduction of Dendy's figure showing the thermal distribution for largemouth bass (*Micropterus salmoides*), walleye (*Stizostedion v. vitreum*) and sauger (*Stizostedion canadense*) through March to October. Here he illustrates the influence of temperature in its control of the general distribution of these fish, and the modification of this distribution caused by low concentrations of oxygen. Poor oxygen conditions on August 16 moved walleye into warmer water, and similar conditions on September 6 moved both walleye and sauger into warmer water. Table III summarizes Dendy's observations for various species of fish.

Salvelinus hybrids (*fontinalis* × *namaycush*) in two Algonquin Park lakes offer a clear-cut example of temperature influencing the distribution of fish. Martin and Baldwin (1958) show (Fig. 3B, 3C) that thermal conditions control the depth distribution of these fish. Thermal stratification in three consecutive years occurred at different depths during the observation period, and the hybrids showed similar differences in their distributions.

EFFECT OF THE THERMOCLINE

Since the thermocline is the boundary between the warm and cold water it has come to be looked upon as a natural boundary in the distribution of fish, to

the extent that we speak of warm- and cold-water fish. The evidence at hand is not sufficient to reach a firm conclusion on the thermocline as a barrier. It may act as a thermal or density barrier. Fry (1939) points out that the sharpness of the thermocline in early summer in Lake Opeongo determines the availability of perch to lake trout. Bardach (1955) related oxygen conditions to perch distribution when he considered the effects of shallow and deep (early and late—Bardach's terms) thermoclines in Lake West Okoboji.

COMPARISON OF LABORATORY RESULTS WITH FIELD OBSERVATIONS

Figure 7 compares the laboratory final preferenda on the left, and the available field observations with available laboratory results on the right. The authority for these data may be found in Tables II and III. Many of the laboratory studies have no counterpart in field observations. They are presented for reference. These studies appear to array themselves on the temperature scale in keeping with general field observations.

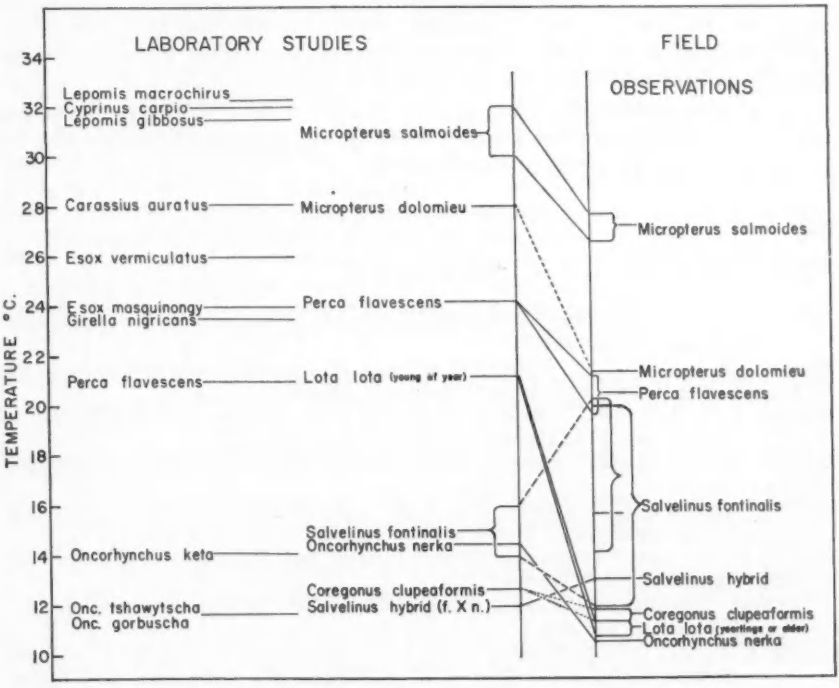

FIG. 7. *Left.* A comparison of various final preferenda as found by laboratory studies. *Right.* A comparison of field observations with laboratory results for a number of species. (See text for discussion and sources.)

Two laboratory final preferenda are presented as a range rather than a single temperature. In these two cases (*Micropterus salmoides* and *Salvelinus fontinalis*) the thermal preference curve paralleled the final preferendum line closely over this range, rather than crossing it cleanly.

The closest agreement between laboratory results and field observations lies within the lower temperature range. *Salvelinus fontinalis*, *Salvelinus namaycush* (not shown in Figure 7—see Tables II and III), *Salvelinus* hybrid and *Coregonus clupeaformis* are surprisingly close in view of the inherent limitations. All other species compared indicate the laboratory studies are consistently too high, Doudoroff (1938) also found this to be the case. The most plausible reason for this is that the laboratory studies are almost without exception of fry or fingerlings. Fry (1937) showed that young cisco tended to remain in warmer water while the older fish moved into colder water. General field observations also point to the fact that the young of *Micropterus*, *Perca* and *Lota* remain in water warmer than that inhabited by older individuals. Field observations of *Perca* (19.7–21.2°C.) when compared with the author's laboratory work (24.2°C.) show a discrepancy, but when compared with McCracken and Starkman's (1948: 21.0°C.) show good agreement. McCracken and Starkman conducted their experiments at a different season (winter), and with fewer fish that were older (two years old or older) than mine. The age differences between the fish used in these two experiments are considered the significant factor.

It is also possible that the discrepancy shown by *Micropterus salmoides* might have been decreased if there had been warmer water available (see Fig. 5) at the time of field observations (Dendy, 1948).

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Climatic Temperature Changes and Commercial Yields of Some Marine Fisheries[1]

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ABSTRACT

A review of the literature suggests need for re-examination of the bases for some reported climatic temperature–fish productivity relationships. In some instances adequate provision does not appear to have been made for changes in the amount of fishing, in economic conditions or in the efficiency of the fishing fleets. Possible fortuitous relationships should be avoided by exhaustive tests of the representativeness of both the temperature and fishery data. They can arise from many sources such as the use of air temperatures to represent subsurface conditions, particularly for short-term periods. Due to the considerable variation in temperatures between stations and between seasonal temperatures at any given station there is a high chance of attaining significant but invalid correlations. Also, the methodology of relating temperature with fishery data, such as time-lagging and correlation analyses, should conform with the life history of the species investigated.

Consideration of the above leads to the belief that any possible effects of climatic-temperature changes upon the Pacific and Atlantic halibut stocks appear to have been overwhelmed by fishing.

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[1]Received for publication March 10, 1958.

J. Fish. Res. Bd. Canada, 15(4), pp. 625–683, 1958.
Printed in Canada.

INTRODUCTION

THE RELATIVE EFFECTS of fishing and natural factors on the abundance of marine species of fish and upon the yields therefrom have been the object of a great amount of study throughout the world. There is agreement that man's impact upon the stocks has introduced an additional element into the already complex and fluctuating conditions under which a species may exist. But differences of opinion as to the relative weight that should be placed upon the effects of the removals by man as opposed to changes that may have been brought about by environmental factors appear to arise chiefly from the incompleteness of our knowledge or lack of quantitative evidence regarding the question.

For many pelagic species, such as the clupeoid and scombroid fishes, it has been usually believed that abundance has been little affected by fishing, natural fluctuations appearing to transcend by far the effects of man. However, lately this belief is being challenged. Hodgson (1957), supported by Cushing and Burd (1957), provides some evidence that fishing has reduced the size of some herring (*Clupea harengus*) stocks. Shimada and Schaefer (1956) have shown that fishing may be a very significant determinant affecting the yield and stock size of the yellowfin tuna (*Neothunnus macropterus*). For some demersal species, particularly the flatfish such as the Pacific halibut (*Hippoglossus stenolepis*) and the Pacific petrale sole or brill (*Eopsetta jordani*), the stocks seem to have been more responsive to fishing than to natural fluctuations (Thompson and Bell, 1934; Cleaver, 1949).

The objective of this paper is to examine the bases for some of the hypotheses that have been presented concerning the effects of climatic temperature changes upon the yields of certain fisheries. It is generally recognized that temperature appears to be a critical factor in geographical zonation, but the available evidence associating the commercial yields of some fish stocks with climatological changes may be questioned. Also, such matters as determination of stock sizes and their maximum utilization cannot be adequately resolved until fishing versus environmentally induced changes in fish populations are each placed in their proper perspective.

Since studies began in 1925 on the Pacific halibut by the International Pacific Halibut Commission cognizance has been taken of the role that fluctuations in the physical and biotic environments may have played in affecting the productivity of the species. Such relationships have been a matter of continuous attention and must remain the object of a very significant share of the research funds available for the study of the Pacific halibut. To be of practical value they must be of a nature which will permit quantitative values being placed upon them.

Regulation of the Pacific halibut fishery has been largely based upon the premise that fishing has predominantly affected the exploited stocks and yields therefrom, and that natural fluctuations have been secondary factors and have been chiefly applicable to short-term changes in stock and in the dependent fishery.

Fluctuations that have already been observed in the halibut stocks can be placed in three categories: those that can be directly attributed to the effect of fishing; those that are an indirect effect of fishing; and those attributable to non-fishery influences.

The major changes and trends in the general level of the halibut stocks and yields have been shown for some periods to be predominantly the direct result of fishing (Thompson and Bell, 1934 and Thompson, 1950 and 1952). An indirect result of fishing can be seen in the changes in the age–length relationship over the past 25 years on grounds west of Cape Spencer which, on first examination, appear to be in keeping with the long-term changes in stock density brought about by the fishery over the same period (Intern. Pacific Halibut Comm. Report 21).

On the other hand, the appearance of individual year-classes or groups of year-classes of above average strength which have exerted short-term and secondary effects upon the yield and over-all population density should probably be attributed to factors other than fishing. Such short-term changes in stock size arising from unusually strong entry of young into the fishable stock have been observed at least three times during the past 30 years in the Goose Island stock (located in Queen Charlotte Sound, British Columbia) and in other stocks off the British Columbia coast. Like changes have also occurred in some of the stocks west of Cape Spencer, Alaska, where year-classes of varying strength have appeared from time to time.

The existence of these secondary but none the less important non-fishery induced changes must be given due consideration in management. For the Pacific halibut, where some of the stocks may be approaching a level of maximum sustainable yield, natural fluctuations could temporarily obscure changes brought about by fishing. At such stock levels gross natural declines or increases in recruitment could temporarily be mistaken as being caused by the fishery. In fisheries management it is of major importance to ascertain what the relative weight of the controllable effects of fishing may be compared to the uncontrollable forces of nature.

To the present authors there recently appears to be some over-emphasis upon the role that climatic-temperature changes may have played in affecting fish stocks. This may well have arisen in counteraction to an earlier tendency to possibly overemphasize the effects of fishing. Such changing attitudes seem to arise chiefly from the inadequacy or inconsistency of research findings. In the Pacific halibut fishery, depending upon the choice of data, both significant and non-significant relationships appear to exist between fishery and some meteorological data. These and the anomalously low fishing rate indicated by the low recovery of tags on grounds west of Cape St. Elias (International Pacific Halibut Commission Rept. No. 25) remain a challenge to continued research.

In this report studies made by others upon the presence of natural fluctuations in Atlantic halibut (*Hippoglossus vulgaris*) and Pacific halibut will be reviewed. Some of the published evidence concerning possible relationships

between climatic changes and fluctuations in several other Pacific and Atlantic marine fish stocks will also be examined.

It is inevitable that the reviews will be critical as we believe that many authors contributing to this subject have not closely examined the adequacy of presently available fishery and hydrographic or meteorological data. However, it must be recognized that though the latter may not have warranted some of the published conclusions, it remains that new evidence might substantiate some of the conclusions. It is not the intent of this report to prove or disprove the presence or absence of relationships between climatic changes and productivity of fish stocks. The purpose is to critically examine the bases for some of the published conclusions on this subject.

Critical Survival Stages

There is a dearth of knowledge regarding the onset of any critical stage or stages of life at which preponderant natural mortality in fishes may occur from time to time. In relating temperature patterns to the survival of demersal fish, the average winter rather than annual temperatures are often considered to be

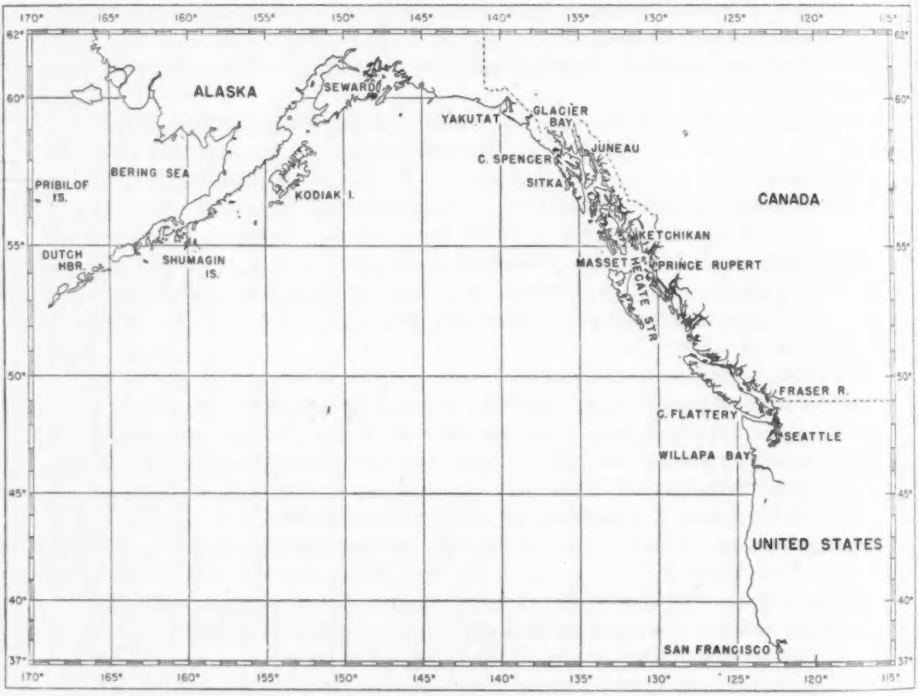

Fig. 1. Map of the Pacific Coast of North America showing important place names mentioned in text.

more critical in view of the fact that the winter months encompass most of the young pelagic life in various species. Some have proposed that the more critical period may be that of maturation prior to spawning (Poulsen, 1937), or the natant eggs and larval stage (Hjort, 1914), or the post-larval period when food requirements may dominate (Hjort, 1926), or the early bottom stages which may serve as prey of larger fish. Marr (1956) found that the scanty evidence available points toward survival of the early life history stages at a constant rate or a constantly increasing rate, rather than toward a critical period. Sette (1943) observed that mortality in the mackerel was substantial throughout the prejuvenile stage. Except in a few instances present knowledge gives little foundation for assuming any one stage of the early life of most marine fishes to be more critical than another. Also, each stage occurs in most species at different seasons of the year, and since trends in environmental conditions, both short and long term, may be very different for each season, it seems that valid linking of the two variables—recruitment to the commercial stock and prior environmental conditions, requires much more knowledge regarding the life history than is presently available. Also, whether smoothed trends or actual values of the paired observations from year to year should be compared would depend upon the manner in which the two variables may be assumed to be interrelated. The choice should not be made on the basis of which gives results more favourable to the hypothesis.

Because the most favourable conditions for survival often differ considerably from those for growth or those for reproduction or for other life processes, Clarke (1954) concluded that for one such condition, namely temperature, the optimum for a species can be only a general concept. He directed attention toward the range of temperatures within which an organism throughout its whole existence functions best.

Relationship between Air and Water Temperatures

Because of the present deficiencies in meteorological and oceanographical knowledge it is often necessary to translate air temperatures—consisting chiefly of short and often broken series of monthly and annual averages taken at land stations often removed from the oceanic areas and subject to local topographic influences—into those of the bottom or the subsurface environment.

Templeman and Fleming (1953) noted that in historical series the locations of observation stations have often not been stable and that comparisons from isolated years are not much use in determining trends, as temperatures in individual years may vary greatly in any period.

It has been demonstrated (Jensen, 1937) and it is generally recognized, that sea surface temperatures usually reflect the temperatures of the overlying air masses. However, even this relationship is not always apparent for certain stations or closely adjoining areas, possibly due to the transport of water into an area from elsewhere. For example, while the trends in air and surface water temperatures at New Westminster, British Columbia (Ketchen, 1956a) and Departure Bay, near Nanaimo, British Columbia (Fleming, 1955) respectively, paralleled each other, the smoothed trends of surface water (U.S.C. & G.S., 1952)

and air temperature (U.S. Dept. of Commerce, Weather Bureau, Annual Summaries for Alaska Section) at Ketchikan, Alaska, at the same time were in opposite direction for at least nine years of the period shown (Fig. 2). These comparisons may be affected by the fact that both Ketchikan and Departure Bay are located on restricted water bodies.

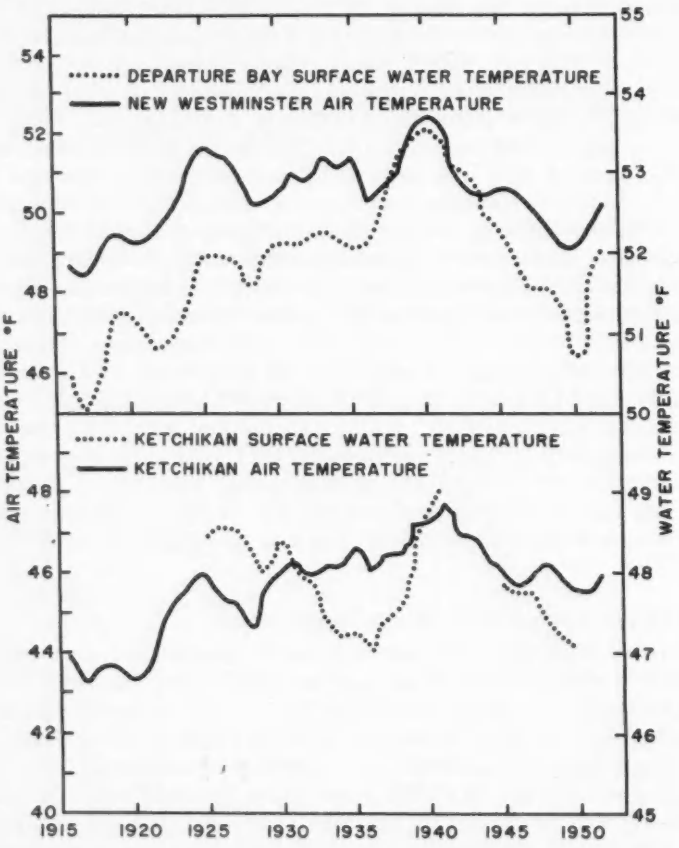

FIG. 2. Comparison between smoothed mean annual surface water and air temperatures at Ketchikan and mean annual Departure Bay surface water and New Westminster air temperatures.

On the north Icelandic offshore coastal area there is a long-term resemblance between sea surface temperature and air temperature, but over shorter terms of 10 to 20 years the trends may be very dissimilar and frequently in opposite directions (Stefansson, 1954, fig. 8).

There is no extensive series of observations of bottom or subsurface oceanic temperatures available for the North Pacific to test the validity of using historical land air temperatures as indicators of subsurface or bottom oceanic values within

the bathymetric ranges of the Pacific species involved in this discussion. There are some North Pacific oceanic observations that suggest a parallelism between temperature changes at various depths. For example, Van Cleve and Seymour (1953) found that winter changes in surface temperatures over a ten-year period showed some agreement with mean values from the 100 to 400 meter levels.

Selection of Representative Temperatures

Some conception of the problem of even developing representative temperatures can be ascertained by examining the summarized 1922 air temperature data for certain North Pacific locations. This year was chosen as it was one of extremely low winter air temperatures in certain months at many northeastern Pacific stations and thus contributed significantly to the sharpness of the trough in the long-term air temperature trends.

The following table from Summers (1923) shows the departures from normal of the 1922 January to April monthly and annual air temperatures in degrees Fahrenheit at a number of stations from Prince Rupert, British Columbia, to the Pribilof Islands, Alaska. It includes departures from normal based on five or more years of record to 1921 inclusive. The stations extend from Dixon Entrance to the Bering Sea and comprise a very large portion of the range of the Pacific halibut.

	January	February	March	April	Annual
Prince Rupert	+2.5	−6.4	−1.4	−0.9	−0.4
Ketchikan	+4.3	−6.2	−0.4	−0.5	+0.1
Fortman Hatchery (near Ketchikan)	+5.2	−9.2	−0.1	−0.4	+0.1
Juneau	+4.8	−6.2	−2.1	−1.2	−0.9
Yakutat	+2.9	−3.3	−1.4	−1.6	+0.2
Kodiak	+3.4	+0.5	−3.0	+0.3	+0.2
Dutch Harbor	+5.4	+1.4	−0.6	+3.3	+1.6
St. Paul Island (Pribilof Island)	+5.6	+7.6	+2.9	+6.4	...

Such great variation in temperatures from month to month and from one part of the coast to another greatly complicates the problem of relating mean temperature changes to any biological phenomenon. During warm periods of long climatological trends some of the coldest months of winter may occur, and similarly during generally colder periods some of the warmest months may occur. In 1922 there was an unusually warm early winter (December 1921 and January 1922) throughout the region and an extremely cold February west to Kodiak but a much above normal February beyond that point, including the Bering Sea.

It is doubtful that extremely cold or unusually warm air temperatures during one month or over a limited period of the year would be immediately reflected in mid-water or bottom temperatures in the oceanic regions where halibut spawn and where the eggs and larvae appear to spend their early existence. Clarke (1954) reported that, owing to the lag in heating, the maximum temperature of the surface water in the North Temperate Zone normally occurs in August; but at a depth of only 70 meters in the coastal waters off New York, "summer" does not begin until November. Jensen (1937) made a comprehensive study of this relationship for the Transition Area (Kattegat region) and found lags of from two to four months between maximum surface and subsurface temperatures. The problem must be additionally complicated by upwelling, currents, and other local

disturbing variables. On the other hand, persistent rising or falling trends of mean annual air temperatures over a period of years could well result in some moderate change in the mean bottom temperatures in the offshore oceanic areas. Whether such changes would affect survival or be merely within the normal range of tolerance of the organism is a moot question.

Nearly any shape of trend can be found in seasonal temperatures, particularly for short-term but also for long-term periods. This is well exemplified in the long series of quarterly surface temperatures compiled by Goedecke (1952, p. 12) for the Helgoland Bight for the years 1872 to 1950. Hesselberg and Birkeland (1944) also showed that for Norway over long periods of years the seasonal trends of air or surface temperatures are quite different from one another—summer temperatures may decline and winter temperatures increase. This seasonal variation is also demonstrated locally in Figure 3, which shows the quarterly mean air temperatures at Ketchikan, Alaska for the years 1930 to 1945. Since any season of the year may be the one of critical survival it is extremely hazardous to conclude that a general resemblance between some trend of seasonal temperatures and stock size indicates a relationship between the two variables.

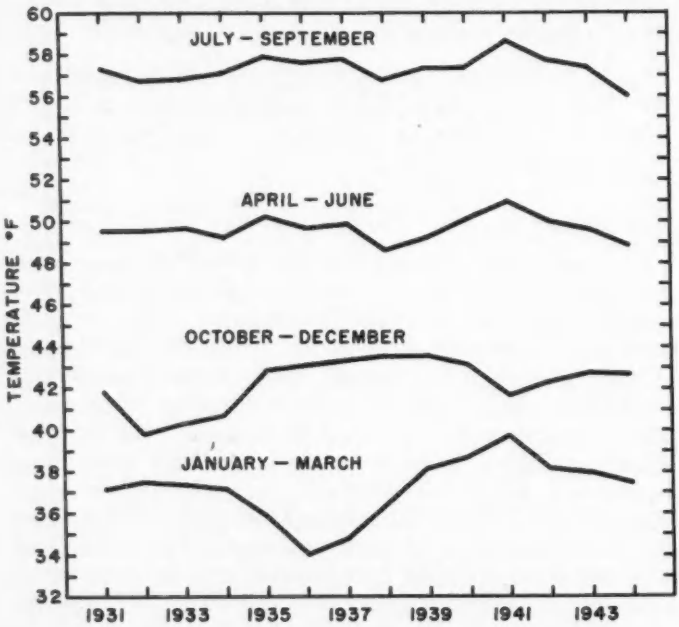

FIG. 3. Ketchikan smoothed "seasonal" air temperatures, 1930–1945.

In view of the present lack of information regarding the physical conditions of survival of marine fishes from the egg to the adult and the absence of knowledge concerning what stage or stages or time of the year an organism may be more sensitive to its environment, relating survival to an annual or some seasonal temperature trend can result in misleading conclusions.

Because temperatures often vary from one location to another within the same general region, great care should be exercised in selecting temperature stations to relate with fishery data. An exhaustive examination of the variability between temperatures at different stations should first be made to determine the representativeness of specific stations or combinations thereof.

A recent paper (Ketchen, 1956a) developed certain temperature and catch per unit of effort data (Fig. 4) for some Pacific Coast marine fisheries to show that long-term changes in air and water temperatures have been occurring in the Pacific area but that important effects of such climatic changes on the stocks of fish may have been masked by the influences of economics and the fisheries themselves. Ketchen felt that suggestive correlations existed between temperature and

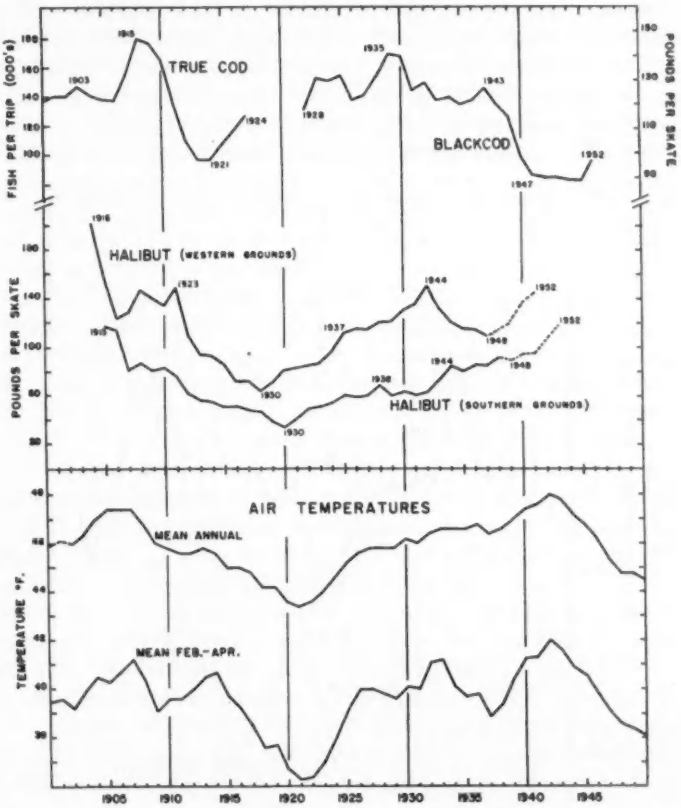

FIG. 4. Masset smoothed air temperatures and their relation to trends of the catch per unit of effort of halibut, true cod and blackcod. For each species the catch per unit of effort data are offset by the number of years equivalent to the approximate median age of contribution to the catch. 1903 on the true cod trend line should read 1910. (Reproduction of Fig. 9, Ketchen, 1956a).

catch per unit of effort of some species even as to details, and that the indicated relationships could not be ignored. Historical air temperatures observed at Masset, British Columbia, situated at the north end of Graham Island (Fig. 1), were compared with changes that occurred during the present century in the catch per unit of effort of the Pacific halibut, blackcod and Alaska cod fisheries whose combined ranges encompass about 2,500 miles of coast from Oregon to the Bering Sea. Methods and data in the aforesaid paper will be examined in detail since this paper is the first of its type pertaining to North Pacific demersal species. The paper points up the paucity of historical meteorological and oceanographical data which authors dealing with this subject in the North Pacific are forced to use.

In addition to the basic question whether air temperatures at Masset have reflected water temperatures over the area considered, there is also the question of how Masset air temperatures compare with air temperatures at other North Pacific stations. In Figure 5 the trends for several individual Pacific stations along with combined figures for the Dixon Entrance to Bering Sea region ('Southern Alaska') are shown. In contrast to Masset temperatures, which show a sharp decline from 1900 to 1922, temperatures at all stations examined from Tatoosh

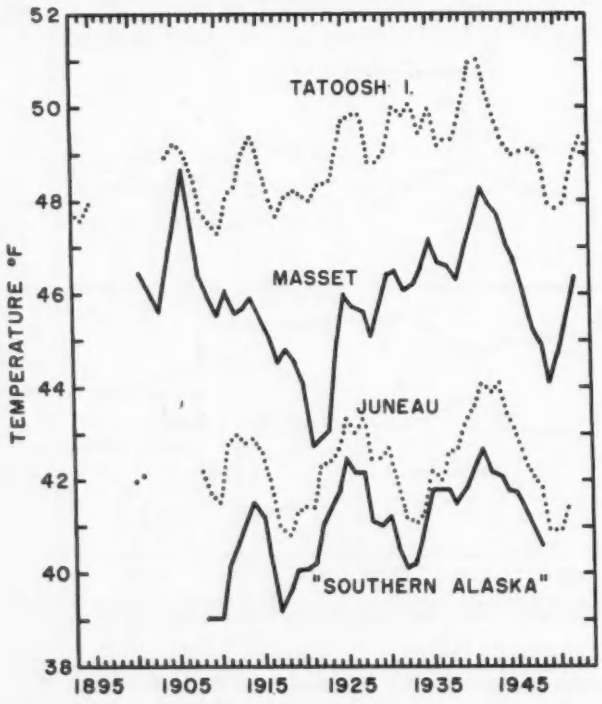

FIG. 5. Smoothed mean annual air temperatures at Tatoosh Island, Masset, Juneau and southern Alaska Division consisting of southeastern, Pacific Coast and Aleutian Island districts.

Island, Washington northward to at least Juneau, Alaska gradually increased, with temporary recessions, from the earliest years on record until about 1940. It may be added that the trends shown by Ketchen for San Francisco, California and New Westminster, British Columbia from 1900 to 1922 also differ from that shown for Masset and generally conform with those of the other northern stations. The earliest comprehensive temperature records for Yakutat and Kodiak, Alaska do not begin until 1917, but they also show an upward trend from that year through at least 1922.

The trough of low mean annual temperatures at Masset centering around the year 1922 was concluded by Ketchen to be peculiar to the northern regions. To extend the representativeness of the Masset "trough" of mean annual air temperatures and of the Masset data in general it was stated that the trough was also evident in data presented by Rounsefell (1930) for Seward, Alaska (about 800 miles northwest of Masset). However, Rounsefell's data for Seward were for the mean March to June temperatures and not mean annual values to which they were being compared. Thus, seasonal data for Seward would not necessarily corroborate an annual Masset or "northern district" peculiarity. Many Pacific coast stations showed a trough of lower temperatures in the early 1920's, yet others did not. A greater depth of the trough for certain stations results from extremely low temperatures in one month of one year at those stations. The depth of the trough is also affected by whether 3-, 5-, or 7-year moving averages are used to smooth the annual temperatures.

Care should also be taken in determining the representativeness of water temperatures. This is shown by Goedecke's (1952) series of surface water temperatures for the north European area. The temperature anomalies at Andenes, Nordoyan and Ona, Norway, and from the area south of Iceland (Region H) and near the Faroes (Region J) are reproduced in Figure 6 from Goedecke. The great differences in trends between stations, particularly prior to about 1920, are obvious and show the need for careful selection of "representative" stations that would encompass the environment of the species under study. Even within a restricted coastal area, such as that of north Iceland, long-term sea surface temperature trends in some months may be very different between locations in close proximity to one another (Stefansson, 1954, fig. 9).

The situation in north-European waters may be analogous to that in the northeast Pacific. Ona, Nordoyan and Andenes, located on the Norwegian coast, lie eastward of Iceland and the Faroes and approximate a geographical alignment such as exists between southeastern Alaskan stations and Kodiak Island. Thus, the choice of "representative" temperature stations to encompass the wide geographical range of the Pacific halibut would be an extremely difficult task. It is improbable that any single station could satisfy the requirements.

Air Temperatures and Glacial Changes

The use of glacial changes to extend the representativeness of air temperature changes may not be warranted. Alaskan glaciers have different histories of advancement or recession depending upon such varied and complicated factors as snowfall accumulation at high elevations, degree of cloudiness, prevailing

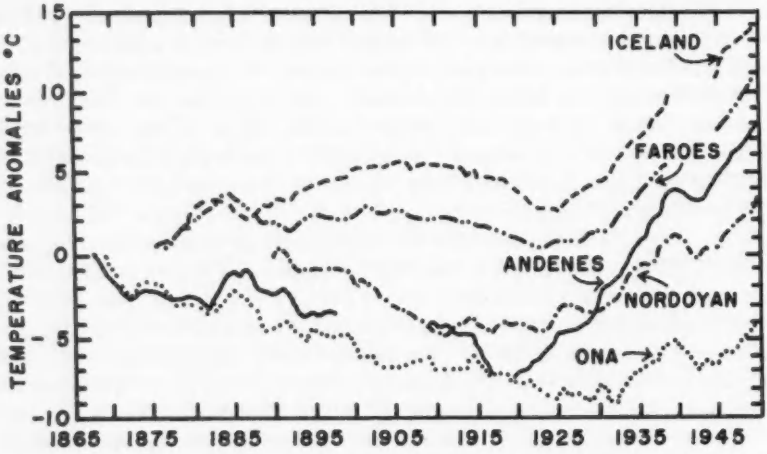

FIG. 6. Cumulative surface temperature anomalies (from the average for 1901–1930) at certain European North Atlantic stations. From Goedecke, 1952.

wind direction, size of ablation area, temperatures (both at low and high elevations), local topography, and many others. Also, recession rates determined from positions of glacier termini represent only a partial picture of the fluctuations which may have occurred in the growth or shrinkage of glaciers in general. Recent studies have shown that a glacier receding at its terminus may not be dwindling in its upper reaches, and conversely, a glacier may be "sinking" in its area of accumulation while its terminus continues to advance (Heusser, Schuster and Gilkey, 1954). Within these two situations there are many possible variations.

Even if the recession rates of the Muir Inlet Glacier as related by Ketchen (1956a) to Masset air temperatures were representative for Alaskan or southeastern Alaskan glaciers in general, their conformance with the land air temperatures at distant stations would have questionable meaning. Field (1947) stated:

> One would wish that this record of ice recession (Muir Inlet Glacier) could be correlated with meteorological observations in the immediate vicinity of Muir Inlet. However, the only available data are from stations at Haines, Skagway, Juneau, Sitka, and Yakutat which are from 30 to 140 miles away and at sea level. These do not record the local changes in temperature and precipitation in Muir Inlet or conditions in the area of snow accumulation at 3,000- to 6,000-feet elevation.

Examination of Field's figure from which the Muir Glacier recession rates were obtained after 1907 shows great differences between the rate of movement of the Muir Glacier terminus and that of the Burroughs Glacier in Wisconsin Inlet, only about 6 miles from Muir Glacier. Between 1926 and 1931 the Muir Glacier receded little (about two per cent of its total 1926 to 1941 recession). During the same time the Burroughs Glacier receded about one kilometer, or over 40 per cent of its total 1926 to 1941 recession. Field attributed the abnormally slow recession of the Muir Glacier from 1926 to 1931 to the shallowness and

constriction of that part of Muir Inlet where the terminus was then located. The rapid recession of the Muir Glacier between 1892 and 1907 is at least partially explained by Field's statement that "after the summer of 1899 a rapid recession occurred, believed to have been accelerated by the great earthquake in September of that year". The earthquake's effect on Muir Glacier may be judged by the fact that it caused the discharge of so much ice into Muir Inlet that points of observation could not be reached again until 1903.

According to present knowledge, the general trend in Alaska since about 1765 has been one of over-all glacial recession except for slight temporary re-advances. However, within this over-all trend there are many notable exceptions. For example, the recent glacial history of the Prince William Sound region differs from the general trend. Within the past 40 years some of the glacier termini there have advanced much further than at any time within at least 500 years (Lawrence, 1950). An illustration of dissimilarity between glaciers is provided by the Taku and Norris Glaciers in the Juneau area which emanate from the same ice field and have termini side by side. Taku Glacier has advanced 3½ miles since about 1900 while Norris Glacier has been receding since about 1916. In contrast to the varying recession rate of the Muir Glacier, the Mendenhall Glacier has apparently receded since 1900 at a rather uniform rate.

In view of the variations in advance and recession rates of different glaciers even when located side by side, the lack of knowledge concerning the exact causes for advance or recession for glaciers in general and any one in particular, and the refusal of Field (the authority on Alaska glaciers who provided the detailed data on Muir Glacier for 1907 to 1946) to attempt to correlate distant meteorological events with the observed recession rates, the use of local glacial changes to expand the significance and representativeness of air temperatures at distant stations is not sound.

Selection of Fishery Statistics

There are usually a large number of methods by which fisheries data can be collected and interpreted, giving a number of different estimates. Thus, the same care should be devoted to examining the validity and representativeness of fishery data as is given to examining temperature data. Whenever possible, catch per unit of effort values should be used rather than production (landing) values. In developing catch per unit of effort data it must be determined whether the unit of effort is reasonably comparable over the period of time covered by the study, and any changes in trend, particularly abrupt or anomalous ones, should be verified by independent evidence that may confirm or deny the statistical data.

Though dealing with marine animals other than fish, the comprehensive and critical treatment of the problem by Dickie (1955) warrants mention as it illustrates some of the difficulties facing workers when using fishery statistics. Dickie compared the relative strength of year-classes of the giant scallop (*Placopecten magellanicus*) with temperatures prevailing at the time they were spawned and concluded that changes in abundance of the stocks resulted from the combined action of temperature and water circulation on the pelagic larvae.

After a critical examination of various measures of stock size, both relative and absolute, the average annual catch per boat of the total estimated fleet from 1936 to 1952 was determined by Dickie to be a rough measure of changes in relative abundance and was correlated ($r = 0.641$) on a 6-year lag basis with September to November temperatures. By the elimination of deficiencies in the original data, it was noted that the adjustment would increase the correlation to $r = 0.723$. It was there concluded that water conditions related to temperature are primarily responsible for fluctuations in abundance of commercially available scallops as measured by the chosen catch per unit of effort.

While Dickie was severely critical of his data, it appears to the present authors that the above relationships with temperature might be tempered by the fact that different estimates of the number of effective fishing vessels in the fleet in one year varied as much as 45 per cent (season of 1949–1950). Also, the "best estimate" of the fleet size was the only estimate available for 8 of the 17 years covered by the study, and in a number of years critical to the correlation, such as 1939–1942, the temperatures were calculated from incomplete records. On the other hand, the temperature relationship may be somewhat improved by weighting the size of the total fleet by the number of fine-weather days available for the period 1941–1952.

In comparing temperature and year-class strength, Dickie stated (p. 847) that no year-classes for 1940 to 1942, the years of lowest temperatures, were detectable in the samples. However, inspection of his length-age data suggests that the 1949 commercial catch, though low, was well supported by those year-classes (p. 846, fig. 14) and that thereafter they continued to contribute significantly to the catch per unit of effort in numbers, and even more so by weight. Also, these year-classes had been previously exposed to some removals as indicated by the high annual commercial catches prior to 1949.

Estimates of stock size based on strip census fishing for the four years 1950 to 1953 (p. 804, fig. 4C) indicate that the stocks on inshore beds had tripled in size and those on offshore ones had declined about one-third. Since the fishery was chiefly prosecuted on the offshore grounds during these years, it may be contended that the adult stock trends as shown by the catch per unit of effort may to a considerable extent be affected by fishing as well as by non-fishery induced recruitment fluctuations. Presumably, the stocks on both offshore and inshore grounds were produced under generally the same prior water temperatures.

In view of the comprehensive system of observation that has been directed to this fishery, it is probable the future will provide quantitative measures as to the relative effects of the fishery and of the environment upon the adult scallop stocks.

Methodology of Relating Abundance with Temperature

Several quantitative methods have been used by various authors to relate abundance with temperatures. One has been to correlate the total number of individuals contributed by different year-classes throughout their existence in

the fishable stock with temperatures prevailing at some particular time during the early life of each year-class. This method usually has no serious deficiencies. A more common method has been to relate temperature to the catch (usually in pounds) per unit of fishing effort for the entire fishable stock a fixed number of years later. This method assumes that changes in the over-all catch per unit of effort reflect changes in survival of one particular age or year-class. The time lag is usually taken as either the age at which the fish become fully recruited or the age of maximum contribution in numbers of individuals to the catch. These latter methods possess deficiencies which limit or invalidate their use in some situations.

An age group which dominates the catches in numbers of individuals or the first fully recruited age group may contribute less poundage than an older age group due to the exponential rate of increase in weight with age. Hence, the technique of assigning the catch per unit of effort, which is comprised of all age groups, to the individual age group which contributes the maximum number of individuals or to the first fully recruited age group is, in some cases, unrealistic.

The magnitude of the error involved in using a fixed time lag depends upon several variables. One such variable is the number of age groups present in the fishable stock; generally the presence of a large number of age groups will cause a greater error than a small number. For example, where recruitment falls to a low level and then continues at this same new low level for an indefinite period, and where the age of maximum contribution to the catch in weight of individuals is, say, three years, then the effects of the low recruitment will not cause a significant drop in the catch per unit of effort until three years after the initial drop in recruitment. In this case a decline will occur in the catch per unit of effort which may properly be attributed to the change in recruitment three years earlier. However, with the continuing same low level of recruitment the catch per unit of effort will continue to decline until the last age group produced under earlier normal survival conditions has passed through the fishable stock. The length of the "transitional period" will depend upon the number of age groups in the catch. During such periods the use of the fixed-lag technique in relating catch per unit of effort with temperatures is questionable.

Another variable which affects the validity of the fixed time-lag technique is whether changes in year-class strength are of a long- or short-term character. The fixed time-lag method has more utility when dealing with stable or long-term trends in recruitment than it has when dealing with short-term changes. For year to year or short-term changes, the sustained effect on the catch per unit of effort of year-classes of "normal" or "above normal" strength after they pass the age of maximum contribution in weight is usually great enough to dampen the effects of below normal year-classes on the catch per unit of effort. With irregular changes in year-class strength the situation becomes more complex, and when coupled with possible changes in other variables, such as fishing intensity, the use of a fixed time-lag can often lead to erroneous conclusions.

A less common method of relating temperature to year-class strength is to compare percentage age composition with lagged temperatures. The use of the percentage method requires the basic assumption that the population size is

practically constant from year to year. Ketchen (1956b) believed that in spite of the fact that the size of the lemon sole population in Hecate Strait fluctuated, it was less misleading to assume constancy in order to determine relative year-class strength than to use catch per unit of effort which was apparently impaired by a lack of constancy in catchability from year to year. Using the percentage age composition method, inverse relationships ($r = -0.706$ to $r = -0.904$) were observed between the percentage strength, as 6-year-olds, of ten successive year classes of lemon sole and the corresponding mean water temperatures for various combinations of 2- and 3-month intervals between December and May six years earlier. The correlations achieved by this method using percentage age composition may be considered suggestive but possess considerable uncertainty as they are dependent upon the validity of the assumption that the population had remained relatively constant, which is contrary to what the changes in temperature over the period of study suggest. Increasing fishing mortalities affecting the various age classes unevenly also might well invalidate the method.

The extent to which the foregoing factors have been considered in studies upon a number of marine species throughout the world is examined in the following sections.

COD

North Pacific Cod

EVALUATION OF ABUNDANCE MEASURES

There is a wealth of detailed information on the historical economic factors and general changes in the unit of effort for the Bering Sea cod fishery since the year 1864 in Cobb (1926) and since about 1905 in the files of the *Pacific Fisherman*. From the detailed tables forming the basis of Cobb's summary table (p. 467) it is evident that there were variable numbers of small 21- to 60-ton gas boats included in the California and Washington fleets during some years along with the regular fleet of 200- to 400-ton schooners. There was also a greatly varying number of small 5- to 20-ton gas boats in the Alaska fleet in some years. The numbers of cod landed per trip used by Ketchen (1956a) to relate to Masset air temperatures apparently included the data of the smaller Alaska vessels as well as those of the large California- and Washington-based vessels.

The inclusion of all craft in computing catch-per-trip values impairs the comparability of any average catch per trip in view of the relatively small total number of regular vessels in the fleet. Also, since the tonnage composition of the regular fleet varied from time to time and the larger vessels of the regular fleet tended to make larger catches, adjustments are needed for this reason. The length of the voyage also could be indicative of fishing success and availability, although it is true that under some special circumstances an abnormally shortened voyage could indicate poor fishing. The length of voyage is a vital consideration in a salt-fish fishery, as within limits the vessels will remain on the grounds until the fare has reached the profit or non-loss level or until they have "wet (used) their salt". This fact may deny the usefulness of the catch per ton or per trip even of vessels of comparable size as a good measure of availability of fish.

The diverse vessels included in Cobb's summary table can be seen in his detailed annual lists of crafts on pages 468 and 484. As an example of the variable composition of the fleet from time to time, the 1910 and 1920 fleets by classes of craft and with their catches were as follows:

	No. of craft	Size (net tons)	Total catch No. of fish
1910			
California	3 Schooners	328 to 376	380,000
Washington	6 Schooners	138 to 252	911,500
Total	9 Craft		1,291,500
Av. per craft			143,000
Av. per sailing schooner			143,000
1920			
California	7 Schooners	281 to 392	918,000
	1 Gas Vessel	115	23,000
	1 Schooner	64	27,000
	2 Gas Boats	21 to 35	39,000
Washington	4 Schooners	171 to 413	465,000
	1 Steam Sch.	217	85,000
Alaska	8 Gas Boats	5 to 17	123,867
Total	24 Craft		1,680,867
Av. per craft			70,000
Av. per sailing schooner			126,000

The necessity of making a proper selection of reasonably comparable vessels in each year is obvious.

In Figure 7 the number of fish caught per trip, as portrayed by Ketchen, and the number caught per-ton-per-day's absence are plotted as deviations from their average values from 1907 to 1924. The two trends oppose each other. We believe only the number caught per-ton-per-day's absence provides a moderately good estimate of the historical availability of cod in the Bering Sea and vicinity. Further refinements of this index of abundance are possible but they are not warranted for the purposes of this paper.

Strong independent corroborative evidence for the greater validity of the catch-per-ton-per-day's absence as being indicative of abundance is found in the following published remarks. In 1921 fishing "was exceptionally good and the vessels got much better fare than usual, the fish being large in size as well as more numerous"(*Pacific Fisherman Yearbook*, 1922, p. 93). A decline in catch-per-ton-per-day's absence from 1907 to 1908 (obscured in Figures 7 and 8 due to smoothing) is confirmed by the remark that "unusually heavy ice and stormy weather (prevailed) north of the pass (Unimak)" (*Pacific Fisherman*, Sept., 1908). Similarly, a drop in the catch-per-ton-per-day's absence from 1913 to 1914 is supported by the remark that "the weather proved quite stormy and much tackle was lost by most of the vessels" (*Pacific Fisherman Yearbook*, 1915). Also, a sharp rise in 1909 finds confirmation in the note that "all of them (schooners) having found fish in great number and having taken good catches in less time than usual" (*Pacific Fisherman*, Sept. 1909, p. 25).

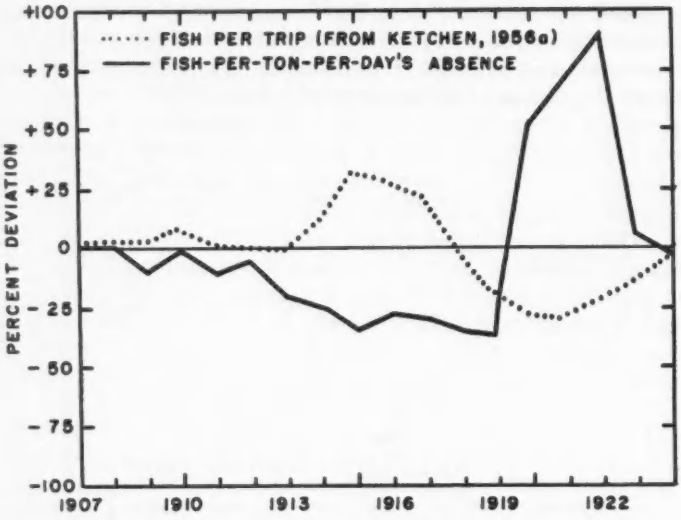

FIG. 7. Yearly percentage deviations from the smoothed average number of Bering Sea cod caught per trip and per-ton-per-day's absence during the period 1907–1924.

On account of the long recorded and detailed history of the Bering Sea cod fishery it may be of interest to examine the available statistical materials for any valid long-term trends in abundance. In Figure 8 the catch per ton and catch-per-ton-per-day's absence for the regular schooner fleet in the eastern Bering Sea is shown for the years 1885 to 1932. The values for the catch-per-ton-per-day's absence for the years prior to about 1900 are probably not representative of the availability nor comparable to later figures due to the few vessels involved in the early fishery. Also, the relationship between net tonnage and catch may well have been different at that time. The trend since 1900 probably possesses some greater validity in spite of changes in the composition and individual design of the schooner fleet that may not be adequately provided for by the correction for tonnage alone. The trends of the catch-per-day's absence for some individual vessels that fished consistently for at least a decade generally parallel and tend to confirm the trend or segments thereof shown for the schooner fleet as a whole.

The almost steady decline in fish-per-ton-per-day's absence may have some reality as a measure of changed availability and may also be related to changes in some or many physical, biological or economic conditions. Unfortunately, the paucity of oceanographical observations in the study area together with a lack of biological information on the cod does not permit an investigation being made of any such relationship. If removals from the stock by the fishery played any part in the decline they were probably a secondary influence. Some of the sharp rise in the fish-per-ton-per-day's absence in 1921 (smoothing obscured it in Figure 8) may be attributed to the fact that the fleet was greatly reduced and

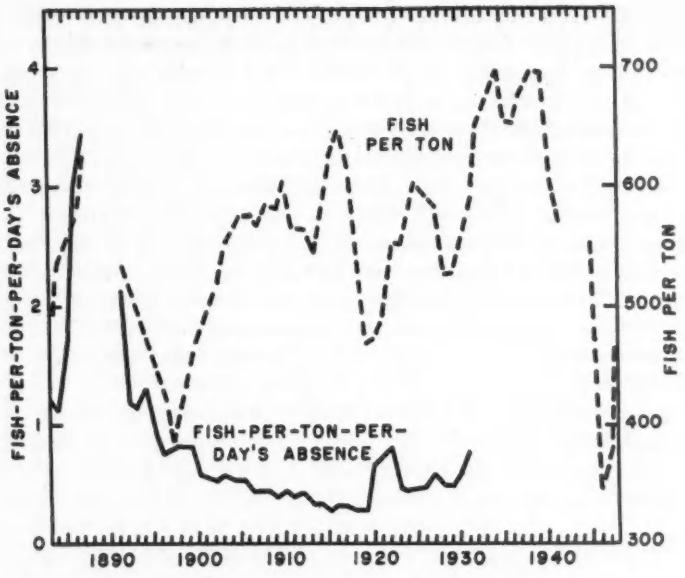

FIG. 8. Smoothed numbers of Bering Sea cod caught per net-vessel ton from 1883 to 1948 and per-ton-per-day's absence from 1883 to 1931 by Washington and California vessels.

the vessels remaining in the fishery during that year of economic depression were probably the more effective ones. The availability of fish and their average size were also very high that year as previously noted (*Pacific Fisherman Yearbook*, 1922, p. 93). The apparent higher level after 1921 can be largely ascribed to the steady growth in the number of powered dories in the California vessels and subsequently in the Washington vessels. By 1929 only one vessel continued without powered dories (*Pacific Fisherman Annual*, 1929). It is not proposed here that the reduced removals of later years contributed significantly to the apparent rise in catch per unit of effort.

The catch-per-ton-per-day's absence cannot be readily determined after 1932. However, since 1933 the number of dories carried per schooner is available which provides an average catch-per-dory-per-season (Appendix, Table V). However, the relatively small size of the fleet after 1933 precludes any judgment being made as to trends except that there was no significant drop in abundance from 1933 to 1949.

DISTRIBUTION AND TEMPERATURE

A possible cod-temperature relationship was investigated by Ketchen by comparing Masset air temperatures with Bering Sea fish-per-trip-values 7 years later. The 7-year lag was chosen on the basis of average age composition of the

Bering Sea cod shown by Mosher (1954). However, on the basis of fluctuating age composition of line-caught cod in other parts of the world, which may also have occurred in Bering Sea, it is doubtful that a fixed lag period would be applicable. It was concluded by Ketchen that even trials with shorter lags did not alter the impression that there was little detailed conformity between the fluctuations in catch per unit of effort and Masset temperature.

It is interesting to note that if the mean February–April air temperatures at Sitka, lying about 150 miles north of Masset but still 2,000 miles from the centre of the historical cod fishery in Alaska, had been used instead of those for Masset a statistically significant negative correlation ($r = -0.58$) would be observed with Ketchen's catch per unit of effort data. This comparison involving the same non-representative fishery parameter but temperatures at another location relatively close to Masset illustrates the different results that may arise from the arbitrary choice of data.

Though his analysis of the cod statistics provided negative results as to any detailed conformity between temperatures and catch per unit of effort, Ketchen believed that the cod of the North Pacific had undergone noticeable changes in abundance and distribution in recent times. This had been also suggested by Ellson *et al.* (1949) who stated with respect to the prospects for trawling in the Alaska and Bering Sea areas that ". . . one of the most interesting facts was the pronounced scarcity of codfish. The local inhabitants stated that while codfish were formerly very plentiful in the Kodiak area, now (1948) they are quite scarce. As far as the exploratory fishing was concerned their scarcity would seem to have been confirmed. . . ." This statement of Ellson (p. 15) was made in respect to the Kodiak area, which has never supported any significant shore station or vessel fishery for cod such as was maintained in the Shumagin Islands region (Cobb, 1926). Furthermore, an examination of Ellson's report shows that the exploratory fishing in the Kodiak area consisted of only 13 60-minute otter trawl drags chiefly between Cape Chiniak to Marmot Island, and 4 drags elsewhere off Kodiak Island in the early part of October under extremely adverse weather conditions.

Ketchen suggested that the declining temperature of the past decade may have shifted the northern limit of the range of the cod to the south, accounting for their increased abundance off British Columbia. On the other hand, many believe that the recent increase in cod fishing off British Columbia by United States and Canadian trawlers has largely resulted from market demand, probably aided recently by the development of the fish-stick trade. Extremely large catches of cod had been reported off the British Columbia coast since the start of the modern Pacific trawl fishery about 1940. However, until recent years this species was discarded or rigid limits were imposed by the buyers upon the amounts to be brought in.

Although there have been many statements made in recent years regarding a scarcity of codfish in Alaskan waters, it is felt that they should be viewed with caution until a scientific appraisal of all the facts is made. Ketchen recognized the difficulty of assuming a change in distribution of the cod in view of the fact

that a successful Bering Sea cod fishery was maintained in the area from 1905 to 1925 at temperatures as low or lower than those prevailing at present.

Arcto-Atlantic Cod

The foregoing remarks on the changed geographical distribution of the Pacific cod directs attention to the North Atlantic where the cod has been stated to be "the classical example" of a change in fishery brought about by altered climatic conditions (Tåning, 1953). Tåning stated that a northward shift in distribution and simultaneous increase in magnitude of the stocks of commercially important species of fish over a series of years has constituted surer proof of a climatic improvement than many of the reported extensions in range of rare exotic fishes or other marine animals. He also felt that fishery statistics yield excellent information upon this subject in spite of obvious deficiencies, particularly in earlier times. However, Gulland's (1956) findings regarding the Icelandic trawl fishery lends confirmation to what has been long suspected, namely, that the historical catch-per-unit-of-effort data for distant-water European trawl fisheries are probably unsatisfactory and that apparent increases in size of stocks which some have related to higher temperatures were the result of inadequate corrections being made in the unit of effort chosen.

Tåning (1953, p. 76) identified a generalized pattern of North Atlantic temperature changes, stating that:

> "we had three rather short warm periods in the North Atlantic area; i.e., about 1810–1823, about 1840–1850, and about 1873–1882, and that the longer and warmer period of our present century, which from a meteorological point of view, perhaps, was traceable initially one and a half centuries ago, or more, first became noticeable about the year 1915, increased in the 'thirties–'forties and, now perhaps is on the wane".

The general hypothesis regarding the Atlantic cod stocks appears to be that as a result of the general warming of the northern regions since about 1920 there has been a significant northern shift of the populations or rise in their abundance in what once were marginal areas. Extension of the hypothesis to include other species finds the evidence somewhat tenuous and even so contradictory as to actually weaken the more comprehensive evidence regarding cod alone.

Traditionally the distribution or availability of cod has always been closely related to temperature. Some feel that the limits to what constitute "cod water" are very narrow but Hachey (1954) shows that the most profitable fishing temperatures reported by a number of observers cover a considerable range and show some contradictions. Also, other factors such as food concentration (Hachey, 1954; Rasmussen, 1955) may be more important in limiting the availability or distribution.

GREENLAND

Dunbar (1946) with respect to West Greenland stated that:

> "There appears to have been a short period of warmer water in West Greenland in the decade following 1880; followed by a colder period represented by the records for 1908,

> 1909 and 1916. By 1928 the conditions were considerably warmer, and there is a reason to believe that the peak of the present warm period was reached in the 1930's. . . . The cold year of 1938, and the signs of a retreat of the Atlantic water at Godthaab during 1942–1944 suggest that the cycle may be falling back to colder conditions. Added weight is lent to this possibility by the increased winter ice of very recent years."

Smed's (1947) data upon West Greenland surface water temperatures for the period since 1876 shows a sharply declining trend since about the mid-1920's, but the level was still above the long-term mean. Lee (1949) noted a decline in subsurface temperatures around Bear Island since 1939 in the European Arctic.

Tåning (1953) noted that the catch of cod by Greenlanders alone increased from a negligible quantity of 350 tons per year a few years prior to 1920 to 18,000 tons in 1951. The total catch from Greenland by all countries in 1951 amounted to 168,650 tons. Prior to 1920 there were negligible landings. While such a many-thousand-fold increase is impressive, it does not necessarily follow that it was caused by an environmental change. The histories of many major fisheries of the world manifest equal and even greater rates of development and over even shorter periods of time. It is typical of that which has occurred many times elsewhere, each with its own time scale, but in the case of Greenland it possessed some rather distinctive features which many authors have almost exclusively related to climatic changes.

Dunbar (1946) observed that the Greenland cod fishery continued to develop through the 1940's probably due to "rise in population and to sustained effort to increase production by various means (rather) than to any hydrographic agency". Furthermore, the Greenlander fleet of non-powered boats has tripled since 1925 and powered craft are four times more numerous than in 1945 (Hansen and Hermann, 1953). Also, the catch by Greenlanders has more than tripled from 1939 to 1950 in face of an indicated steady decline in surface water temperature (Smed, 1953). The foregoing facts suggest that conclusions regarding the dominant effects of climatic change upon the yields should be examined.

Furthermore, the random incidence of successful year-classes which can occur during generally favourable or unfavourable climatic periods can also result in temporary changing levels of yield. But, if random, they should not be considered a resultant of the long-term climatological trend. For example, in West Greenland where there may be a waning of the warm period, an extremely successful year-class (1947) appears to have entered the fishery and will give major support to the catch as has occurred with other strong year-classes in the past (Hansen, 1949). While it appears that the recent appearance in the West Greenland catch of cod of the good 1947 year class was predictable from the June bottom temperatures prevailing on Fylla Bank in 1947 (Hansen and Hermann, 1953) and that there are indications of a general relationship between such bottom temperatures and survival of other broods, it must be demonstrated that the variations in June bottom temperatures parallel the many other indicators that have been used to show climate changes such as annual surface water temperature (Smed, 1947) and distribution of storis or drift ice. Also, a varying and indeterminate proportion of the commercial-sized cod in Greenland waters

from year to year apparently has consisted of fish which were hatched at Iceland and later migrated to Greenland. Such fish of non-Greenland origin should be excluded from correlation analyses between year-class strength and temperatures on Fylla or anywhere else in Greenland.

The very early attempts at fishing in Davis Strait have often been related to past climatic conditions but the evidence both of such attempts and of climatic conditions has been scanty and largely circumstantial. It is unlikely that the aboriginal fishery would reflect any changes in availability of fish as there was no consistent incentive nor survival need for the sparse native population to engage in cod fishing. To some degree it was actually discouraged (Jensen, 1925). Penetration from the outside into the area was also proscribed and, for non-resident or non-Danish fishing enterprise in the region, the legal and technological conditions were almost impossible until very recent years (Steffansson, 1942).

The sporadic efforts to establish an industrial production of cod in West Greenland in the nineteenth and in the early part of the present century likely would have occurred during summers or periods of favourable weather or ice conditions. Thus, apparent historical coincidences of availability or of scarcity of fish with climatic conditions, good or bad, have naturally become established. There was no continuing economic pressure to establish local or foreign industrial fishing in the area as the production from the home waters of Norway, Iceland, Faroes and the almost legendary Grand Banks usually more than satisfied the world export demand for salt cod. In the latter areas the fleets were not faced with the obstacles of weather, ice, short season, and an inhospitable coast sparsely inhabited and practically closed to foreign trade as in Greenland. No small wonder that the area was not intensively exploited until the most recent times.

BARENTS SEA

The Barents Sea is another important area where climatic changes have been stated to have had a dominant effect upon the stocks of fish and their productivity, particularly of cod. Tåning (1953) noted that the catch of cod in the Barents Sea by English trawlers increased from an average of 16.5 tons per hour in the period 1924 to 1928 to 72.6 tons in the period 1947 to 1951, and his grouping of the data suggested that the expansion of stocks during the past quarter of a century had been steady.

Examination of the English annual trawl catch per unit of effort values (landings per day's absence) for Barents Sea cod since 1906 (Fig. 9) shows that there was a generally rising trend from an almost negligible level in 1906 until 1926. Thereafter until about 1932 there was a decline. A very sharp rise then occurred attaining a high pre-World War II level. After World War II another very abrupt rise occurred, but since 1949 there has been a decline. (The landings per 100 hours of trawling had declined by 1953 to the 1936 level.) It is evident that such spasmodic changes in stock level are not what should be expected from gradually changing climatological trends. From 1906 to 1926,

largely prior to the so-called warm period, the catch per unit of effort, though at a low level, tripled. Thereafter, there was no increase for seven years even though the warm period had begun in the 1920's. Practically all of the rise in the 27 years since 1926 occurred within two very short periods—1934 to 1937 and 1947 to 1949—a total space of seven years. Such a pattern of change is probably the result of many factors of which climatic trends may be of only secondary significance.

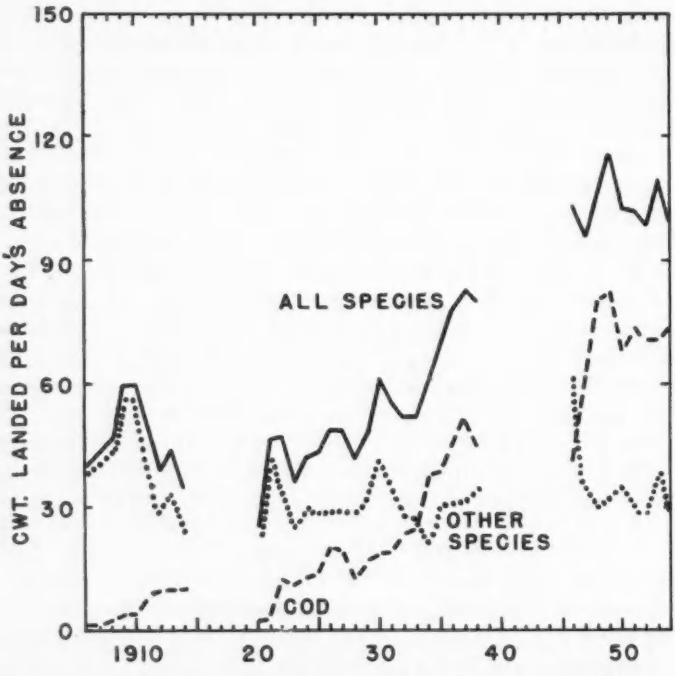

FIG. 9. Landings of cod, species other than cod, and of all demersal species per day's absence for British first-class steam trawlers in the Barents Sea, 1906–1954. Source: Ministry of Agriculture and Fisheries of the United Kingdom, Sea Fisheries Statistical Tables.

During the colder first quarter of the twentieth century demersal species other than cod, including plaice, haddock and halibut, dominated the English Barents Sea trawl catches. Since the latter species are considered warmer-water species than cod it is difficult to assume that cod were relatively scarce on the grounds because of low temperatures. It is more probable that cod were not sought after intensively at that time. By the early 1930's when the productivity of the plaice, halibut and haddock stocks had declined, the cod began to represent an increasing share of the total trawl catch. Cod were then being more sought after, probably to offset the loss of yield from other species.

Also, the sharp increase in apparent relative abundance of cod after 1933 and to some extent even earlier must be heavily discounted by the fact that the means of production were undergoing great changes. More efficient vessels, super trawlers, were being added to the fleet, seriously impairing the comparability of catch per day's absence. There was an increasing use and continuing development of the V-D and other trawl gear that vitiates the index based only upon 100-hours trawling as a comparative historical measure of abundance.

On the basis of Gulland's (1956) partial corrections of catch per unit of effort data for cod at Iceland (Fig. 10), it is more than probable that a similar treatment of the Barents Sea data shown in Figure 9 would remove indications of any increase in productivity, thus invalidating the catch per unit of effort data of English trawlers referred to by Tåning.

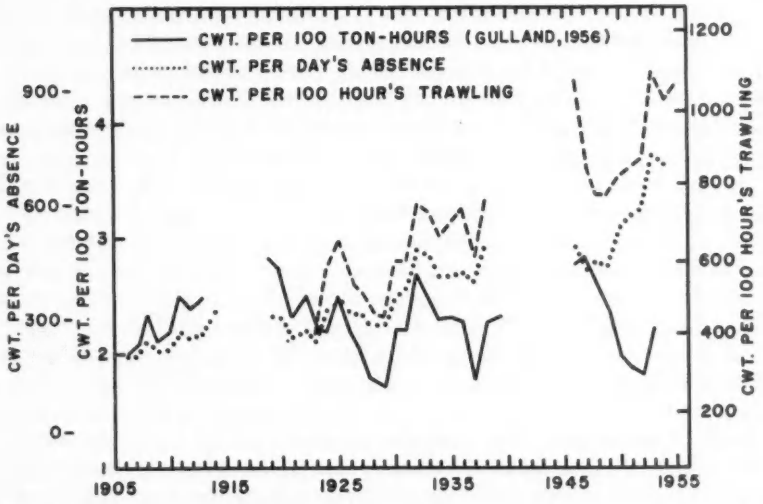

FIG. 10. Comparison of Gulland's measure of catch per unit of effort with previously accepted values for Iceland-caught cod by British first-class steam trawlers.

The temporary post-World War II rise in cod catch per unit of effort also might well be attributed to reduced fishing in the war years, as the increase has not been sustained and there has been a decline to 1954. Furthermore, the random occurrence of good or poor individual brood-years that may occur independently of any secular climatic change can play an important role in changes in the yields of cod for a considerable period after their first appearance in the catch.

The basic productivity of any area should not be assessed by examining a few isolated occurrences or species that may appear to support one or another viewpoint. If the stock densities or yields of all species involved are examined individually and collectively, a more satisfying result would ensue. This is

particularly true when dealing with a trawl-net fishery capable of concentrating on some or neglecting other species from time to time.

The catch per unit of effort of all demersal species by the English vessels from Barents Sea is shown in Figure 9. The catch per day's absence remained generally level for the 23 years from 1906 to 1929, regardless of climatic changes. While there has been an increase to the present, it is now only about twice as high compared to the four-fold increase for cod alone noted by Tåning. Most of the increase in apparent yield per unit of effort of cod has occurred during a time when temperatures have been declining, not increasing, in the general area. Lee (1949) stated that water temperatures between 90–200 fathoms west of 19°E. longitude around Bear Island since 1939 are lower than those in the 1920's and 1930's and are in agreement with the increase in ice since 1940.

Furthermore, the apparent increase in the catch per 100 hours trawling and landings per day's absence for all demersal species in Barents Sea will probably disappear, as in the case of the Iceland-caught cod, when full and proper corrections can be made for changes which have occurred in the efficiency of vessels and gear. It is also noteworthy that the total demersal fish yield of all countries from the Barents Sea in several recent years is not significantly greater than 20 years ago, immediately prior to World War II.

On the basis of the above information, particularly that regarding the unsatisfactory measures of stock size, the current belief that the yield or size of stocks of demersal fish in the Barents Sea have been preponderantly influenced by long-term climatic changes must be re-examined and placed in proper perspective. Fishing in such distant waters as the Barents Sea and particularly Greenland has been made possible due to the technological developments of the past 30 to 40 years. Mechanical refrigeration, oil rather than coal for generating steam, dieselization, fathometers, electronic positioning devices, and many other navigational aids all have aided in the profitable expansion of the range of fisheries. The warming of the waters may have played a far less important role than is generally accepted in affecting the pattern of stock changes and of annual yields. Also, while it is true that warming of the seas could increase productivity through enhanced growth, increased recruitment or migration of adults, it is also true that the more clement weather would facilitate fishing.

The foregoing material should indicate the need for caution in judging the past, the present and the future productivity of the Pacific and Atlantic cod. Some coincidence between climate and yields should not be allowed to militate against a balanced understanding of the manifold forces affecting the fisheries. This is particularly true in view of the defects in the fishery data (Gulland, 1956) upon which many hypotheses have been based.

PLAICE

BARENTS SEA

In northern latitudes the plaice, a warmer-water species than cod, presumably should have reacted to warming of the seas even more favourably than the cod. Yet this species apparently received no benefit from the more salubrious

conditions prevailing in the Barents Sea as the yield and catch per unit of effort have declined except for two typical temporary increases resulting from the respective "Kriegsschönzeiten" or wartime respites from fishing. As the catch of this species declined along with the catch of equally valuable haddock and halibut, the catch of cod increased, most probably due to the conscious compensatory effort of the fishermen. Also, to maintain the over-all monetary value of the catch, the increase in the catch of the less valuable cod would have to be relatively high.

Tåning (1953) believes that the decline of those species susceptible to increased fishing does not detract from the general conclusion regarding the cod. It may be true to some degree that one species and not another may respond to a climatic change, or that for one species and not another the effects of fishing may extinguish the effect of a beneficial environmental change. However, in the Barents Sea it seems more probable that the decline in the more valuable plaice, halibut, and at times haddock, was the immediate and chief cause for the increased concentration upon the cod. This shift of emphasis from one species to another has occurred so often in various trawl fisheries throughout the world as to be almost axiomatic, and the factor of relative availability of each species has, more often than not, been a secondary element in the shift.

SOLE

NORTH SEA

The increase in yield of the sole in the North Sea, with the Danish catch increasing from 200 tons in the 1920's to about 3,000 tons in 1951, is represented (Tåning, 1953) as also being indicative of a stock change in that area associated with the change in climate. While this increase in Danish production is spectacular, it will be shown that it does not represent the over-all situation nor does it necessarily reflect a climatic trend.

In Figure 11 are presented a number of statistical components of the North Sea sole fishery, as published by the International Council for the Exploration of the Sea (*Bulletin Statistique*, 1905–1953). It is evident that the Danish sole catch and the proportion it represents of the North Sea total production is very low; and that the absolute level of Danish production was inconsequential throughout the entire early recorded statistical history of the fishery, and only increased to present proportions at a very recent date and within the space of two years, 1950 and 1951. Such abrupt changes are not indicative of what would occur as a result of the long-term climatological change. Also, the inconsequential production of the Danish fishery during the half century prior to 1949 would probably not be a good measure of the species' productivity during that historical period. While the sole landings by Denmark increased about 12-fold, landings of sole by all countries increased about 3-fold. Furthermore, in both instances the increases occurred after World War II respites from fishing.

The recent abrupt increase in abundance of sole was first noted in the autumn of 1949 and was apparently due to the sudden influx into the fishery of a large number of recruits from the 1947 year-class (Margetts, 1950; Wimpenny,

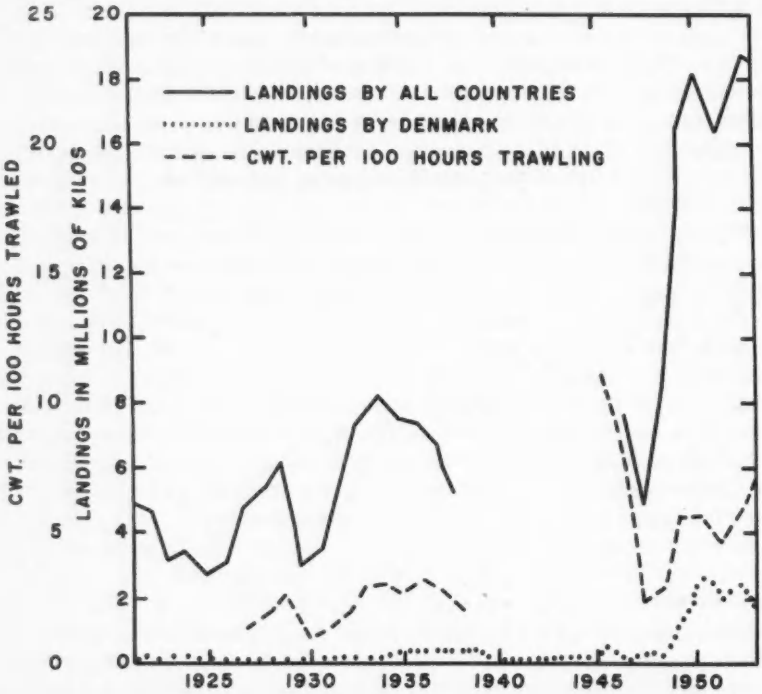

FIG. 11. Landings of sole (*Solea vulgaris*) from the North Sea, by Denmark and by all countries, together with catch per unit of effort for British first-class trawlers.

1950). The effect on the fishery of this unusually strong year-class was great enough to maintain the new high level of production through at least 1953. However, it already appears that the 1947 year-class is no longer able to sustain this level of production and Wimpenny (1956) looks forward to considerable fluctuations in the stock in future years due to the occasional appearance of particularly successful year-classes. Also, Margett's observation that the unusually successful 1947 year-class spawned shortly after a period of exceptionally cold weather in the North Sea to an extent may be incompatible with the warming theory. The sharp increase in catches in 1932 and 1933 also probably arose from some earlier abundant year-class.

EUROPEAN HERRING

Tåning (1953) referred to increases in the herring stocks at Norway, in the Baltic Sea and at Greenland, with a corresponding extension of fishing, and as in the case of the cod considered them the results of climatic change. Actually, it is probable that factors other than climate were more important determinants of the catch levels used by Tåning in judging the size of the herring stocks.

European herring production has been influenced by many economic forces, and these along with the effects of great advances in the techniques of herring fishing, such as Asdic, fathometers, planktonmeters and subsidized scouting, must be evaluated and the changes in yield accordingly discounted before attributing any increases in catch to changes in climate. Complex environmental changes other than climate *per se* have also played a large part in determining the catch levels at various historical periods of the fishery (Devold, 1955). Also very important has been the apparently erratic appearance of extremely successful individual year-classes which can arise from propitious circumstances in one year regardless of the trend of climatic conditions. Such random occurrences can markedly alter the trend of catch for a considerable number of succeeding years irrespective of prevailing environmental conditions.

BALTIC AREA

In the Baltic proper, according to the Bulletins Statistiques of the International Council for the Exploration of the Sea, there was a generally level trend of herring production from the early 1900's until 1925, after which the annual catches rose moderately until about 1939. Thereafter the trend was slightly downward to 1952, though the decline did not reach the level prevailing prior to 1925 (Figure 12). In 1953 and 1954 a sharp increase occurred. This pattern of production change cannot be related to the general warming of the European seas since the mid-1920's or earlier, and to a degree is contrary to what was postulated by Tåning. The sharp rises in the years 1953 and 1954 are also inimical to the climate theory and probably only reflect either a sharp increase in fishing due to economic factors or to the appearance of an unusually abundant year-class or higher availability. .

Examining the combined production of adjoining and connecting waters, namely the Kattegat, Skagerak and Belts, over the same period reveals that production fell from a high level existing between 1906 and 1920 and continued at about the same lowered level until the late 1940's (Fig. 12). Only in 1954 did the catch reach the early high 1910 level. Thus, the long-term trend of herring yield in this general region appears to be unfavourable to the general warming theory, and the rise in 1954 alone should not be so related. Due to the relatively close proximity of the Baltic, Kattegat, Skagerak and Belts areas and their possible common dependence upon the influx of Atlantic water, the combined catch from all these areas is also shown in Figure 12. The high production from 1907 to 1919, the sharp fall to 1920, the fairly steady yield to the late 1940's, and the sharp increase in two years, 1953 and 1954, do not conform to the warming hypothesis. Furthermore, the large catches during the first two decades of this century occurred during a generally colder climate in northern Europe than has existed in recent years. The early catches were also made with far less effective instruments of capture than used today.

NORWEGIAN SEA

Herring production from the important Norwegian Sea area (Fig. 13) remained about level from 1909 to 1925, increased slightly to 1928, and fell from 1929 to

1949. During the years 1951 and 1954 a new high point was reached. As in other regions, the variations in yields do not appear to be in accord with the general trend of climate change (Fig. 6).

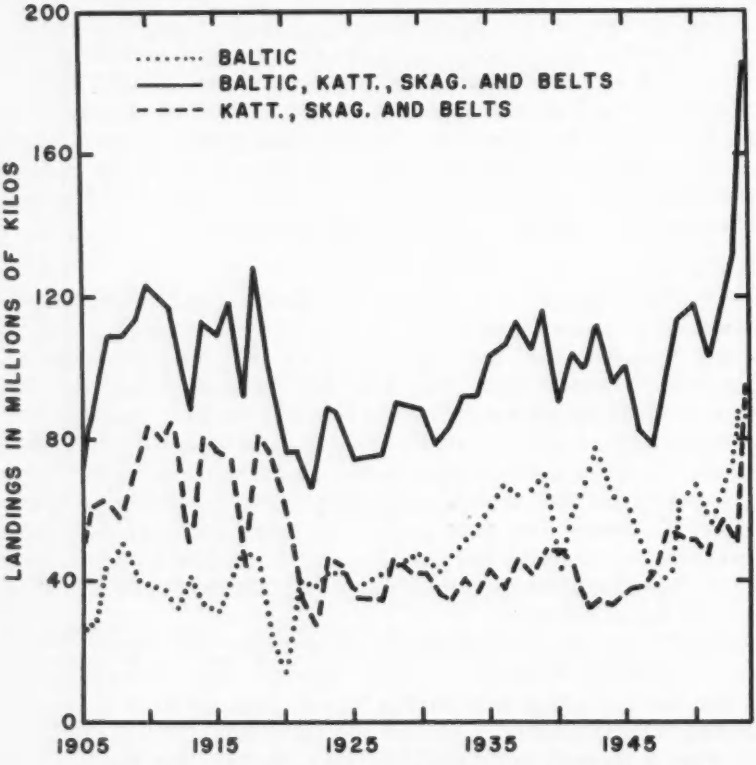

FIG. 12. European herring production for several regions, 1905–1954.

NORTH SEA

The annual yields of herring from the North Sea immediately prior to World War II were not much higher than in the early 1900's (Fig. 13). Since the level rose within the space of about 4 years, in the late 1930's, and most of the increase was in the Norwegian share of the catch, it should not be attributed to any long-term climatic change. Were the latter the case it would have to be assumed that fishing power remained constant and that the warmer climate benefited only the Norwegian fleet in the North Sea area.

WESTERN ATLANTIC FISHERIES

In a study of marine animal abundance and climatic variations on the Newfoundland Grand Banks and off Labrador, Templeman and Fleming (1953) examined the relationship between the landings of several species and air

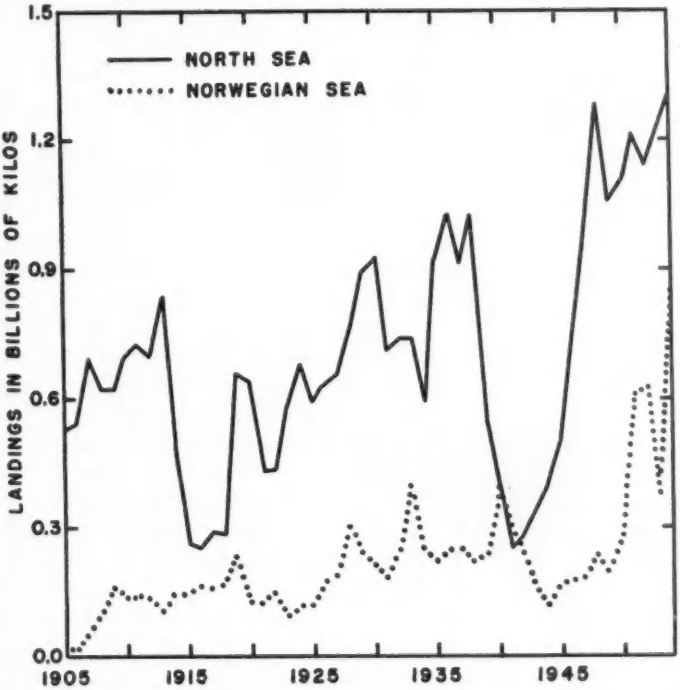

FIG. 13. North Sea and Norwegian Sea herring production, 1905–1954.

temperatures at St. John's, Newfoundland for the period 1921 to 1953. By implication they concluded from the latter that there was a gradually rising trend in water temperatures since the 1870's and 1880's, with the past 20 years almost all above the average mean temperatures of the whole period (1870–1951). Examination of their figure 1 permits an alternative interpretation; namely that there was a rising trend from 1870 to 1890, a decline thereafter to the 1920's, then another rise. The latter interpretation is supported by water surface temperatures compiled by Riehl (1956) for the ocean waters off the southeast coast of Newfoundland. This interpretation also approximates more closely that ascribed to the subarctic region immediately north of the Newfoundland and Labrador area (Dunbar, 1946; Tåning, 1953). However, as in other coastal shelf areas in the world, the water temperature trends often vary greatly between immediately adjacent ocean regions (Fig. 14, based on Riehl, 1956). Consequently, it does not appear that inshore water temperatures or land-air temperatures would provide too reliable indications of trends for distant or even adjacent offshore water areas.

The St. John's air temperature trends since 1870 and St. Andrew's, New Brunswick, water temperatures since 1920 were related by Templeman and

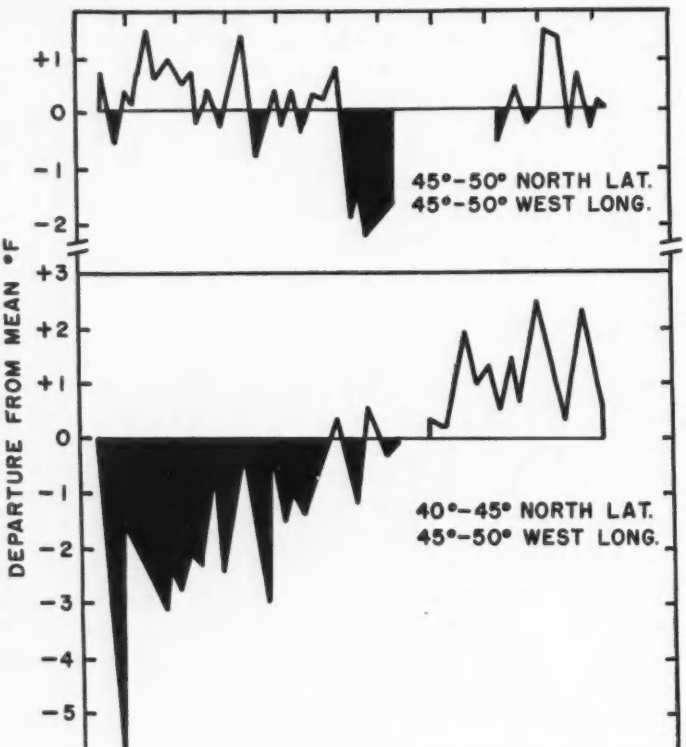

FIG. 14. Long-term annual surface water temperature trends in two adjacent areas near Grand Banks, Newfoundland. From Riehl, 1956.

Fleming to exports of mackerel from Newfoundland, the Newfoundland catch of live lobsters, annual evaluations of the abundance of squid and exports of salted cod-fish.

In a careful study of the effect of climatic trends on the distribution and abundance of certain marine animals in New England waters, Taylor *et al.* (1957) concluded that a recent general increase in temperature has not been accompanied by any obvious alteration in the composition of the fish or invertebrate fauna of the Gulf of Maine region. However, they did suggest that a northward shift in the centre of abundance and distribution of mackerel, lobster, menhaden, whiting, and yellowtail flounder had occurred during the

recent warmer climate. The authors gave critical consideration to deficiencies and errors in available climatological and fishery data used.

LOBSTERS

With respect to the catch of Newfoundland live lobsters, Templeman and Fleming noted that the trend of production had declined steadily from 1890 to the mid-1920's, but that in the recent 20 years there had been a fluctuating but on the average progressive increase in catch. Also, since the early 1920's the three prolonged periods of below average temperatures were felt to correspond fairly well with decreases in the lobster catch. It was concluded that the catch fluctuations were due to changes in catchability in response to temperature levels and not necessarily due to changes in abundance.

On the basis of Templeman and Fleming's interpretation of the temperature trend as being gradually increasing since the 1870's and 1880's, the decline in lobster production from 1890 to the 1920's is to a degree inconsistent with the further observation that the decreases in catches since the early 1920's corresponded fairly well with periods of below average temperatures. A more consistent but no more satisfactory hypothesis could be developed by accepting the present authors' interpretation that the temperature trend from 1890 to the 1920's was downward and that it rose thereafter.

Taylor *et al.* (1957) concluded that optimum conditions ceased to exist for lobsters south of Cape Cod about the middle 1920's, and that conditions began improving for lobsters in the area north of Cape Cod after 1940. They presented landing statistics for Maine, Massachusetts, Rhode Island, and the "Middle Atlantic States" together with January–July differences in surface water temperatures at Boothbay Harbor, Maine. The years since 1904 were included for the Rhode Island landings and those since 1918 for the other areas. For these periods a relationship between temperature and lobster landings was postulated. Consideration of landings prior to those discussed by Taylor *et al.* shows that they were at least as high in Maine and Massachusetts from the mid-1880's to 1900 as they were in the 1940's, despite the fact that the 1880's and 1890's were characterized by lower temperatures than existed in the 1940's.

In view of the abruptness of the increase in lobster catch in the early 1940's and probable effect of wartime demand, it seems possible that more important factors than temperature may be involved. This seems particularly true in the Maine data, as Taylor *et al.* stated that the Maine catch per unit of effort showed no increase for the years 1939–1946, which included the period of rapid rise in total catch.

The close relation shown between landings of lobsters in Rhode Island and surface water temperatures at Boothbay Harbor, Maine from 1904 to 1949 may be fortuitous in view of the fact that landings in three other regions, namely Maine, New Hampshire and Massachusetts, taken individually or collectively, for the same years, do not show any such correspondence. These latter states are closer to Boothbay Harbor than Rhode Island and together account for many times the Rhode Island lobster production.

Cod

Newfoundland cod production from 1870 to 1920 increased with a decline or increase in temperature, depending upon one's interpretation of the temperature trend for this period. Also, the pronounced decline in production since 1920 has occurred in the face of the development of a well-defined warm period. In view of such anomalous results Templeman and Fleming (1953) concluded that many other factors were responsible for fluctuations in the catch of cod.

Squid

Templeman and Fleming felt that the habits of the squid would associate this animal with rather warm water. However, they noted that there were more periods of scarcity and greater than average scarcity since 1930, which encompasses most of the recent warm period, than in the 15 years prior to that time. They stated that they were unable to draw inferences regarding possible long-term effects of water temperatures on the abundance of squid.

Mackerel

Templeman and Fleming (1953) stated that the recent increase in exports of Newfoundland mackerel appeared to represent an increase in fish population, presumably due to a recent warm period. Examination of their data shows that only in the 7 years since 1947 has there been any significant production of mackerel, while the recent warm period has been in general effect since the late 1920's, a period of about 25 years. For example, temperatures were relatively high between 1935 and 1945 with very low yields of mackerel. Also, historically there were several short warm periods of 3 to 4 years duration between 1870 and 1904 when little mackerel was produced.

In Newfoundland the catch tripled from 1946 to 1947. It declined about 50 per cent by 1949–1950, then was doubled by 1952, and the catch in 1954 was only about one-third of the 1953 total. These drastic year-to-year changes appear to be what could be expected from changes in availability or in market demand.

While climatic conditions may have contributed to the increased availability of mackerel off Newfoundland, we believe that other factors, probably those associated with the general post-war expansion of the economy or some random incidence of winds affecting the water masses may have been far more responsible for the greatly increased but very variable commercial production of recent years.

The yields of the mackerel fisheries in different parts of the world have been subject to great fluctuations both over the short and long term, and no simple or single explanation has yet been given. Long-term changes in the yields of the Canadian and United States mackerel fisheries prior to 1931 were critically reviewed by Sette and Needler (1934). They noted that the trend of catch was the result of a multiplicity of causes, such as changing economic conditions, new methods of fishing, expansion to new grounds and natural fluctuations in abundance. The occurrence of extremely successful year-classes such as the 1923 brood had a profound and sustained effect upon the yield. As in the case of many

other species, great fluctuations can occur in the yields from the occurrence of unusually successful individual year-classes. Among mackerel, these have occurred in some particular years due to propitious wind conditions (Sette, 1943) and were not necessarily related to changing climatic trends.

In the abstract of the paper by Taylor *et al.* (1957), the statement that mackerel catches (New England) show a relation to air temperature fluctuations in data extending over a period of 130 years may convey an impression that does not seem to be in the body of the paper. While a statistically significant correlation was observed from 1820 to 1890 between New Haven, Connecticut air temperatures and landings of mackerel three years later, only a weak tendency for the landings to vary with temperature was observed from 1890 to 1925, and after 1925 the landings and temperature fluctuations were quite out of phase. Taylor *et al.* also stated they could see nothing in the temperature record to account for the sharp drop in mackerel landings after the mid-1880's.

The present authors compared annual mackerel catches (U.S. Atlantic) between 1880 and 1930 (Sette and Needler, 1934) with surface water temperatures for July–September (Riehl, 1956) in the area inside and immediately offshore from the Gulf of Maine between 40°–45° N. latitude and 65°–70° W. longitude. The July–September period was chosen because it is the period of maximum occurrence of mackerel in the fishery. The comparison yielded a non-significant correlation ($r = -0.15$) which generally conforms with the findings of Taylor *et al.* for a similar time period, although they compared New England mackerel landings with New Haven, Connecticut air temperatures three years earlier.

The authoritative study of Sette and Needler (1943) judiciously leaves the question of specific cause or causes of catch fluctuations in Atlantic mackerel unanswered. If a relationship between temperature and mackerel abundance is to be demonstrated, it seems that it should have been more noticeable during the recent period when temperatures rose to a new higher level than during the earlier years (1820–1890) when, although fluctuating, the long-term trend of temperature was relatively level. Also, both temperature and fishery data in recent years should be more reliable. Even during the years 1820–1890 the use of a fixed 3-year lag to effect a statistical correlation between catch and temperature throughout may be questioned in view of Sette's (1933) findings regarding the wide variability from year to year in the contribution of the different year-classes to the catch. Sette showed that from year to year the catch may be dominated by different year-classes ranging in age from 1 to 5 years, and further that there are both persistent and transitory types of broods.

Taylor *et al.* apparently did not decide whether increased catches of menhaden north of Cape Cod in recent years were related to the warming of inshore waters there. They noted that the actual abundance of menhaden north of Cape Cod since 1945 is not accurately reflected by catch figures, due to the mobility of the menhaden seine fleet. They also noted that surface water temperatures at Boothbay Harbor over the period 1906–1949 have probably been sufficiently high for the presence of menhaden every year.

WHITING

Taylor *et al.* (1957) based the decline in the Connecticut–Rhode Island total whiting catch since 1943 and in the New York–New Jersey catch since 1947 upon the hypothesis that the coastal waters south of Cape Cod have become too warm for whiting to be present in abundance (p. 333).

Examination of the changes in total catch of whiting by pound nets (rather than by the vessel fishery used by Taylor, where there could be some doubt as to the origin of the catches due to the mobility of the vessels) shows that the magnitude of the decline was nearly as great to the north of Cape Cod as to the south and almost equally precipitous. This does not support the warming hypothesis. The decline also occurred in both regions within the space of very short periods, but not the same periods. The south of Cape Cod, namely New Jersey, decline took place between 1945 and 1948, 4 years later than in the Massachusetts region north of Cape Cod. This timing is the opposite of what might have been expected of the climate factors presumed to have been involved. An environmental change would be expected to have effect first in those areas of more critical survival, which in case of whiting appears to be south, not north, of Cape Cod as judged by the relative historical productivity of the two regions. Also, the abruptness of the declines is not in accord with what one might expect to result from a gradual climatological change. It resembles more what might have arisen from some cataclysmic mortality of adults both south and north of Cape Cod, or from some drastic widespread failure in recruitment to the inshore commercial stocks of one or more important year-classes, or from some market whim. Climate changes may have had but a very minor influence.

Northerly extensions or shifts of range of a number of marine species are noted by Taylor *et al.* as being indicative of warming of the waters. While this may have occurred it seems that proof of the required assumption that equal opportunities existed for observations to the south as well as to the north of the original range would be extremely difficult to demonstrate. The significance of apparent changes in range depend upon whether the changes in distribution are sustained over a period of time or are merely the result of a number of short-term visitors. Accumulation of records of occasional visitors over a period of years could give rise to pseudo-relationships and conclusions.

PACIFIC BLACKCOD

In addition to the Pacific cod and other species, Ketchen (1956a) tested the relation between the catch per unit of effort of blackcod and Masset air temperatures. About three-quarters of the catch per unit of effort data were for the Canadian fishery off southeastern Alaska and the remainder for the northern coast of British Columbia.

Ketchen's conclusion that there was a good negative correlation in considerable detail between the catch per unit of effort (in pounds) and the February–April air temperature at Masset 6 years earlier cannot be reconciled with Figure 4 which shows that only one portion, 1943 to 1948, of the lagged trend of catch per unit of effort declined with rising February–April temperatures, while the two remaining main segments of the trend, 1928 to 1935 and 1935 to

1943, tended to show a reverse relationship. A test of the actual relation between the two variables given in Figure 4 provides a non-significant correlation coefficient ($r = -0.307$). The visual examination of the trends and the non-significant value of the correlation coefficient do not suggest to the present authors a possible temperature-catch per unit of effort relationship. Catch per unit of effort values for the extensive blackcod fishery off Cape Flattery (Bell and Pruter, 1954), lagged in the manner used by Ketchen, were examined by the authors for the years 1918–1952 and they revealed even less apparent relationship with nearby Tatoosh Island air temperatures or any other series of Pacific coast air temperatures examined. It has been previously indicated (Bell and Pruter, 1954) that changes in the catch per unit of effort in the Cape Flattery region can be ascribed to changes in the fishery.

HALIBUT

Eastern Atlantic Halibut

There have been a number of statements made as to the effect of natural fluctuations in the stocks upon the production of Atlantic halibut. Huntsman (1953) stated that natural fluctuations in the abundance of fish are well attested and are evident in the takes of halibut on both sides of the Atlantic, and on this basis Huntsman felt that natural changes in the abundance of Pacific halibut were to be expected.

NORTH SEA

In examining the North Sea fisheries for the effects of natural fluctuations upon the yields, Huntsman (1948) observed a sharp increase in halibut landings in 1914 and noted that "other factors as well as fishing were operative" upon the stocks. As such sharp changes in yield are not expected from a species with the longevity of halibut, the reality of the increase in landings might have been questioned. Also, there were no known changes in fishing effort to account for the much higher yield in 1914.

The Annual Report of the Scotland Fishing Board for 1914 reported a total of 46,512 cwt. of halibut or 5,209,344 pounds from all fishing areas, of which 17,156 cwt. or 1,911,472 pounds were indicated as originating from the North Sea. The 1914 Statistical Bulletin of the International Council credits 2,324,000 kg. or 5,123,490 pounds of the Scottish receipts to the North Sea, which was 98% of the total Scottish halibut catches recorded by the Statistical Bulletin of the Council from all areas. It may be noted that in 1913 and in 1915 only 36% and 17% respectively of the total Scottish halibut catch came from the North Sea. Thus, on a basis of the sharply altered ratio in 1914 and due to the magnitude of the amounts reported it would appear that the North Sea area was credited with almost the entire Scottish catch that year. The official Scottish reports show that only 17,156 cwt. or 1,911,472 pounds should have been so credited. Removal of the difference of 3,212,028 pounds reduces the 1914 North Sea halibut catch by all countries to a "normal" level of 2,879,282 pounds. This suggestion of a presumed natural fluctuation in Atlantic halibut is thus relegated to a tabulating error.

FAROE AND ICELAND

Other evidence believed indicative of natural fluctuations in Atlantic halibut was presented by McIntyre (1952) who made an extensive analysis of the Scottish trawl and line catches of halibut from various North Atlantic areas for the years 1930 to 1949. McIntyre observed that on the Faroe grounds the Scottish trawl catch per unit of effort had declined in 1942 and 1943 from the higher 1940 and 1941 level in spite of the relatively low war-time fishing intensity by Aberdeen vessels, and it was concluded that the higher 1940–1941 level could be projected back to good brood years of 1937 and 1938. The 1940–1941 high trawl catch per unit of effort could also be projected forward to a higher Scottish liner catch per unit of effort in 1943 and 1944 from older fish of the same year-classes. A similar situation was observed on the Iceland grounds for Scottish vessels except that the projection into the liner catch per unit of effort was not apparent until 1945–1946.

The conclusion that the higher catch per unit of effort at Faroe and the roughly similar situation on Iceland grounds in 1940–1941 were due in part to a natural fluctuation in the halibut stock resulting from good brood years in 1937 or 1938 may be true. However, there appears little justification for the final concluding statement of the paper, namely:

> "Roughly similar increases took place on other grounds, and, although Graham (1948) attributes a somewhat similar increase in the early nineteen twenties to 'the benefit of wartime protection' it seems probable that the high yield obtained after 1939 may be due not so much to the reduced fishing effort, as to natural fluctuations in the stock."

This wording minimizes the effects of First World War closure upon the stocks and suggests that the effects of Second World War restriction of fishing were secondary to those of natural fluctuations, though more conservative statements elsewhere in the paper by McIntyre suggest that while the change in stocks ". . . was possibly due to some extent to the reduced fishing, there are indications that this was certainly not the only cause." Indeed, natural fluctuations probably have occurred, as they have in the Pacific halibut, but their effects probably were short term and subordinate to those caused by the variations in the fishery itself.

McIntyre's conclusions as to the relative effects of fishing and natural fluctuations upon the stock may also be questioned by reasons of the parameters utilized. He used only the fishing intensity and yields of the Aberdeen fleets in judging the effects of fishing upon the several stocks. This procedure would be valid only if the activity of the Aberdeen fleet in each area remained proportionately the same each year in the grand total for all countries. The latter was not the case. For example, the Aberdeen fleet's Icelandic production varied from 4 to 45 per cent of the annual total by all countries during the period of study, 1930 to 1949, not including the war years. The yield and intensity data presented by McIntyre thus are only reflections of the Aberdeen fleet's varying participation in the Iceland fishery and should not be considered indicative of the total forces to which those stocks have been exposed. It would be the changes in the total amount of fishing and the combined catches by vessels of all nations to which the stocks would be responsive, not to the variable representation of the Aberdeen fleet in the fishery.

The third variable presented by McIntyre, namely the catch per unit of effort both of Aberdeen trawlers and liners, may be usable provided it represents a random sample of the stocks. Since the halibut is an extremely small component of the total trawl catch of demersal fish, averaging under one per cent in case of the English trawl landings from Iceland from 1930 to 1949, there seemed good ground for McIntyre's doubt (p. 7) that the trawl effort in any area uniformly sampled the stock each year and in a random manner. The liner catch per unit of effort may be a better measure, as halibut represented a larger proportion of the total catches of each voyage. However, there is a general correspondence in the shape of the trends of the catch per unit of effort for the English and for the Aberdeen trawlers, suggesting a limited acceptability of the latter data. McIntyre's annual catch per unit of effort values for the years 1930 to 1936 are the same as those given by Jespersen (1938) which were obtained by averaging individual monthly values, thus giving equal weight to each month. Presumably the remainder of McIntyre's values for the years 1937–1949 were determined the same way. Provided the monthly means are stable and based upon sufficient data, there could be no objection to such a procedure. However, examination of the monthly values and the amount of Aberdeen fleet data upon which the annual catch per unit of effort values at Faroe were based makes the catch per unit of effort data of questionable significance, particularly for certain individual years whose values are presumed to indicate a natural fluctuation.

The paucity of the Faroe data may be indicated by the Aberdeen liner catch per unit of effort and landings from Faroe waters for 1940 to 1944, which were as follows (1942 not available):

	1940	1941	1943	1944
Average catch per 100 lines in cwt.	14.3	8.4	73.8	75.4
Landings in pounds	358,400	33,600	224,000	369,600

The total annual liner catches from Faroe grounds, even equally distributed through each year, would on the average only represent about 3,000 pounds per month in 1941 to 31,000 pounds per month in 1944. Unstable monthly values of catch per unit of effort would probably be inevitable in 1941 with such small amounts of fishing and could not be particularly reliable in other years. The latter is borne out in McIntyre's Table VIII. Even with 5-year monthly averages for the period 1940–1944 the August value of catch per unit of effort is 37 times that of January while in the other 5-year periods between 1930–1949 August values vary only from 4 to 7 times that of the respective January values. Though the monthly catch per unit of effort values for individual years are not available in the paper or in the published fishery statistics for Scotland, it can be expected that they would reveal an even less stable condition than shown in the 5-year periods. Also, the indices of catch per unit of effort used for the Aberdeen trawl catches of halibut may lack comparability, as was found by Gulland (1956) for the Icelandic trawl-caught cod.

Thus, it is evident that the independent parameters for the Aberdeen fleet alone, namely yield and intensity, and the derived variable, catch per unit of

effort, may be of limited value for representing what has occurred in the Faroe halibut stocks and possibly other stocks.

The European halibut fishery over the past 50 years, both on the long-fished grounds such as those in the North Sea and on more recently fished grounds such as at Greenland, provides many instances where declining or rising trends in catch per unit of effort have been almost invariably associated with increases or decreases in the removals by man. Each ground also manifests the now classic reaction of demersal stocks resulting from two major wartime closures or "Kriegsschönzeiten". The following account of the Icelandic stocks exemplifies the process.

According to the Statistical Bulletins of the International Council, the production of halibut from Icelandic grounds fell from a level of almost 8 million kilograms in 1907 to less than 4 million in 1914 (Fig. 15). These early heavy removals were followed by a marked decrease in the catch per unit of effort by liners (Scottish Home Dept., Scottish Sea Fisheries Statistical Tables) from about 50 cwt. per 100 lines fishing in 1911 to about 20 cwt. in 1915. Greatly reduced fishing during World War I was followed by a pronounced rise in abundance and in production for a few years after the war. However, the effect of the large unrestricted post-war removals was soon reflected by a decline in the line catch per unit of effort which reached a level by 1930 which was only about one-third as high as that existing immediately after World War I. From 1919 to 1927, the period of relatively high post-war abundance, liners dominated the Icelandic halibut fishery. After 1928 and until 1940, a period of reduced abundance, trawlers emerged as the dominant element when the landings of halibut by that gear were about three times as great as the line landings. The fact that trawlers are far less dependent on halibut for their earnings than are liners (less than 1 per cent of the total catch from 1930 to 1949 of British trawlers in Icelandic waters consisted of halibut, compared to 12 per cent of the British line catch) may largely explain the pre-emption of the fishery by trawlers during this period of lowered abundance. The emergence of trawlers as the main producers corroborates the decrease in abundance indicated by the decline in the line catch per unit of effort.

The abrupt reduction in total removals during World War II again resulted in a very sharp increase in the line catch per unit of effort immediately after the war. This pronounced rise in abundance was again reflected by the supplanting of trawlers by liners as the dominant element in the fishery. Comparable catch per unit of effort values for liners are not available in published statistics after 1949; but that the line catch per unit of effort has already fallen, as it also did shortly after World War I, is suggested by the fact that by 1953 the trawl landings again exceeded those by liners.

Clearly, this repetition of events in the fishery and in the stocks of halibut must be associated with the periods of changed fishing. Each time a reduction in removals was followed by a sharp and temporary increase in abundance and production and the emergence of liners as the dominant element. And each time the high level of abundance and total production soon fell again and trawlers supplanted liners as the major producers.

Thus, the major fluctuations in abundance of the stock and changes in the fishery may be largely attributed to the extent of man's removals. Such natural fluctuations in stock size as may have occurred were not of sufficient magnitude to impair this conclusion, and must be considered subordinate to the effect of the fishery. The sequence of events is so consistent that one may predict the future of the fishery from its past history, something that cannot be done on the basis of environmental considerations.

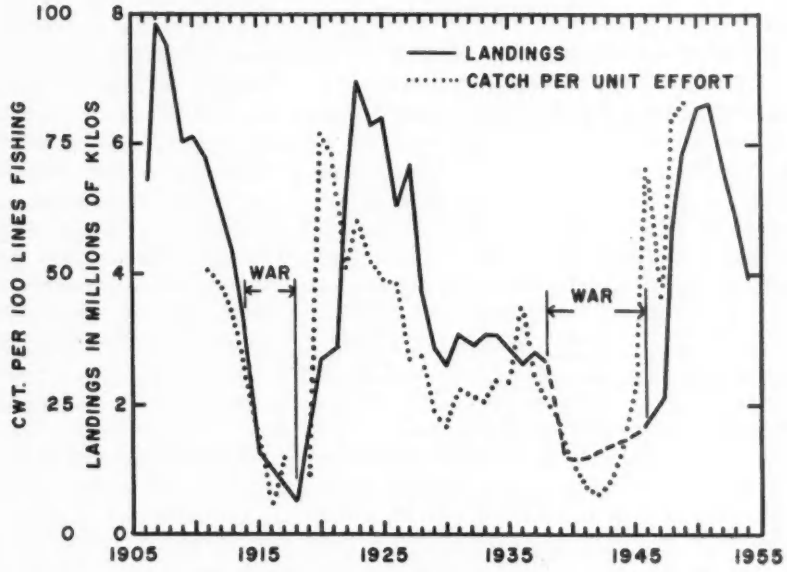

FIG. 15. Total landings of halibut from Iceland grounds by all countries and catch per unit of effort for British liners landing in Scotland.

GROWTH AND TEMPERATURE CHANGES

Sigurdsson (1956) observed that the halibut in Faxa Bay, Iceland, showed an increased growth rate since 1909 and concluded that the reason seems to be the rise in temperature brought about by climate change. It was also stated that the amount of material was insufficient for proving whether this has been the case, but it was felt that much spoke in favour of the role that temperature may have played.

Examination of the temperature and fishery data in Sigurdsson's figure 4 shows that in addition to the possible scarcity of data there are also inconsistencies. While the trend of temperatures shown for Vestmannaeyjar and Stykkishólmur both tend to rise from 1908 to the late 1920's, subsequently the two trends are in opposite directions for the remaining 25 years of the period of observation. Such differences between stations in the same general region are also noted seasonally for the north coast of Iceland (Stefansson, 1954).

Inspection of Sigurdsson's figure 4 for the period 1908 to 1938 shows an inverse relationship between stock density, as shown by the experimental trawl catches, and the size of the 2- and 3-year-olds, which appears to be as good as the direct relationships referred to by Sigurdsson between the size of 2- and 3-year-olds and temperatures at Vestmannaeyjar and Reykjavik. Observations of stock density after 1938 were made in only three years—1939, 1946, and 1948, too few to establish a trend; and the high stock level in 1939 could be attributed to the influx of unusual amounts of Atlantic water into Faxa Bay (Jesperson, 1948) or to the fact that survival conditions were unusually good for the 1937 and 1938 year-classes. The declining level of stock density suggested by the experimental trawl catches is to some extent confirmed by the long-term declining trend in the catch per 100 hours of fishing, uncorrected for Gulland's findings, of British trawlers landing in Scotland from Iceland in the years since 1915. It is to be noted that a considerable proportion of the Icelandic fishing of the English trawl fleet occurs in Faxa Bay itself. Thus, data for the Icelandic fishery as a whole probably reflects the conditions in Faxa Bay alone. It is most probable that adequate corrections for changes in the efficiency of the fleets and the effect of wars would emphasize this long-term decline in stock levels. It also appears that the long-standing dispute regarding fishing by foreign vessels in Faxa Bay has stemmed in part from the decline in the stocks of halibut there (Jesperson, 1948).

As Sigurdsson (1956) pointed out, further judgments regarding reasons for the observed change in growth rate must await additional information not only upon temperatures and stock density but also upon fluctuations in the food supply and in the numbers of competitors.

Growth changes in the Pacific halibut have been observed on grounds west of Cape Spencer (Intern. Pacific Halibut Comm., Rept. No. 21) which, on first examination, appear to be somewhat parallel to the long-term air temperature trends there. However, on grounds south of Cape Spencer such parallelism does not seem to exist. More observations and analyses will be required before any judgment should be made on the question, both for the Pacific and other halibut stocks.

Comparison of European and Pacific Halibut Fisheries

The dominant effect of fishing upon halibut stocks can also be demonstrated by comparing the production histories of the unregulated European Atlantic fishery with the controlled fishery of the North Pacific. Statistics for the North Pacific are from Bell, Dunlop and Freeman (1952) and from International Pacific Halibut Commission Reports No. 18, 20, 21, 22 and 24. European data are from the International Council for the Exploration of the Sea, Statistical Bulletins 1905–1953, in a number of instances confirmed and supplemented by the individual statistical reports of some contributing countries.

The latter information was necessary due to some apparent omissions of landings of vessels in "Foreign Ports" in the Statistical Bulletins of the Council prior to 1928. This situation resulted in the omission of the 1926 and 1927 halibut landings in England by foreign vessels such as the Norwegian motherships from Greenland. In 1928 and 1929 such landings were included, and in 1930 the motherships appear to have changed to British registry and

are included in the English domestic figures. This is further substantiated by the fact that in 1930 the receipt of halibut from "foreign vessels" in England declined to 521,024 pounds from 2,448,320 in 1929, 5,484,192 in 1928, 4,302,368 in 1927, and 2,085,888 in 1926. Of these amounts the following poundage was shown in the English tables to have been caught by "other methods", that is, other than by liners or trawlers:

Year	Caught by "other methods"
1926	1,733,200 pounds
1927	3,798,032 "
1928	5,126,464 "
1929	2,060,576 "

The Norwegian catches from Greenland recorded in the International Council Statistical Bulletins were as follows:

Year	Caught by "other methods"
1928	5,103,649 pounds
1929	1,873,910 "

Since these figures approximate in magnitude the aforementioned English figures for the same years, it can be concluded that the "other methods" catch is that of the Greenland mothership fishery which was by vessels of Norwegian registry. On this basis it is possible to correct the International Council's statistics of European landings of halibut prior to 1928. These revised figures also clarify several inconsistencies in the trend of landings as published by the Council. For example, practically no Greenland-caught halibut was shown in 1927 but motherships were known to have been operating in that area. Examination of the statistical reports of each country also does not permit the presumption that this poundage had been included in their records.

The following additions as derived from English and Scottish data have been made to the total halibut landings reported by the International Council for Europe:

1923	846,384 pounds
1924	495,152 "
1925	654,080 "
1926	2,418,080 "
1927	4,449,968 "

It is believed that for countries other than Scotland and England any reported landings of halibut by foreign vessels would be relatively limited and that for years prior to 1923 this would be true for all countries including Scotland and England.

The annual catches in each fishery are shown in Figure 16 for the 50 years since 1905. During this period there have been no controls imposed upon the European fishery except for two pronounced reductions in fishing due to World Wars I and II. In addition, autonomic economic controls have become less and less effective down through the years. This has arisen from the fact that an increasing proportion of the European halibut catch is being taken by trawlers whose fares include only a relatively small proportion of halibut. In such a fishery the stocks of halibut can be driven to very low economic levels of yield such as existed in the North Sea in the late 1930's. On the other hand, vessels using line gear such as the European "liners" and the regular Pacific Coast halibut vessels depend largely upon the halibut in their fares for their earnings. They must cease to fish whenever the stocks fall below the profit level.

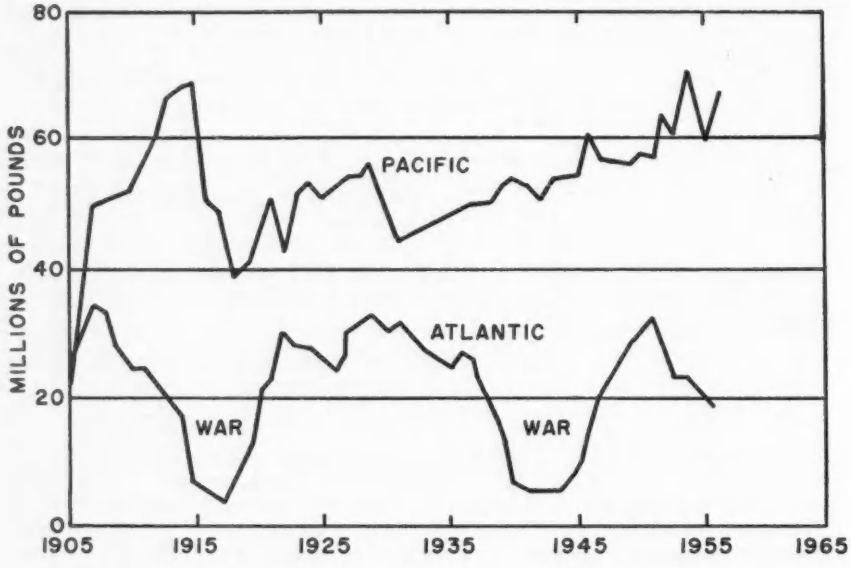

FIG. 16. Eastern North Pacific and European halibut landings, 1905–1956. (Dressed, head-off weight in pounds not including catches of Greenland halibut, *Rheinhardtius hippoglossoides*.) Total 1955 and 1956 European landings are estimated from landings by major producing countries.

As with the Pacific fishery prior to 1930, the fleets in Europe had brought all areas into production in a vain effort to offset the decline in yield from the older grounds. By 1929 in both the Pacific and European Atlantic the fishery was covering the entire range of the commercial stocks. Thereafter the total yields commenced to decline in both regions. In the Pacific fishery the decline in total catch was accelerated by economic conditions in 1930 and 1931 which reduced the amount of fishing on some parts of the coast. Since the beginning of regulation in 1932 the trend of catch has steadily been raised and may be approaching that of maximum sustainable yield for some areas.

In Europe the trend of the total catch after 1930 was downward, in spite of a rising demand as shown by the increase in the average price of halibut in England whose market absorbs over 75 per cent of the European production. The rise in price of competing species showed lower percentage increases. The downward trend in the European production was temporarily halted in 1936 by the development of a short-lived net fishery for spawning halibut in Norwegian fjords in which 2,500 fishermen participated during the winter of 1936–1937 (Devold, 1938). Since 1945, after the respite due to World War II, the trend of the European catch rose as the fleet was rebuilt and fishing was undertaken on the stocks accumulated during the war.

The post-war rise after 1918 and subsequent decline after 1930 has already had its counterpart after World War II; and the decline has been more abrupt than during the 1925 to 1935 period, because the Greenland–Labrador regions have not sustained the total catch to the extent that they did from 1925 to 1935, nor is it believed that they will do so. The uncontrolled European production will probably level off at between 15 and 20 million pounds, or less, annually, a marginal production caught by trawl gear and consisting chiefly of juvenile fish under 5 years of age. Due to the great complexity of trawl fisheries and particularly those of North Europe, it is unlikely that any practical measures can be envisaged in the foreseeable future to alleviate this condition. In the Pacific halibut fishery the trawl capture of halibut is prohibited, and the results of regulation to date point to the attainment of a maximum sustainable yield in the near future, probably in the vicinity of 70 to 75 million pounds annually, and consisting almost exclusively of adults ranging from 6 to 25 and more years of age.

The sharp contrast between the production trends in the two fisheries over the past 30 years provides further convincing, though circumstantial, testimony to the preponderant effect that fishing or its control has had upon the yields of halibut, the influence of natural fluctuations being subordinate to the effect of man's removals.

Western Atlantic Halibut

Though Huntsman (1953) implied that there were also indications of a major natural fluctuation in western Atlantic halibut, off Canada, no specific evidence for it can be found in the literature. McCracken (1956) does not suggest that there have been any natural fluctuations, but rather that year-to-year changes in the level of catch have been the result of economic factors influencing the amount of effort directed to the fishery. He believes that the present Canadian Atlantic fishery is in a more or less balanced stage with available stock but suggests that there are some unfavourable shadows in the picture.

West Greenland

It has been suggested that the vicissitudes of the Davis Strait fishery for halibut, as for cod, have been associated with climatic changes that have occurred in the region over the past century. The incidence of the 19th century American salt-halibut fishery and of the modern fishery have been specifically related by some of the more salubrious climates existing at each period.

The statistical material of Scudder (1883) on the Greenland salt-halibut fishing, consisting of individual American boat catches, indicates that halibut were more or less uniformly abundant throughout the period 1866 to 1881, and, according to Jensen (1925) continued so through the "nineties". Also, if the stock fished in 1866 was a local accumulation, the abundance must have existed for some time previously as only large, older fish were used for flitching. It is thus unreasonable to assume that immigration of halibut into the area occurred simultaneously with the onset of fishing in 1866. It is most probable that halibut were available in quantity at least throughout the latter half of the 19th century, warm or cold periods notwithstanding.

The American salt-halibut fishery in Davis Strait was discontinued prior to 1900 due to the imposition of heavy duties (Jensen, 1925) and a decline in demand for the product. No evidence is available that lack of fish was a factor. Also, the influx of Pacific halibut into the eastern United States markets after 1888 probably added to the declining demand for the salted Greenland product.

In view of the foregoing there is little basis for claims that changes in halibut productivity showed any correspondence with changes that have been presumed to have occurred in the climate. It seems that other factors than the presence or absence of halibut were more responsible for any changes in the extent of the fisheries during the last half of the 19th century.

After World War I declining halibut production in European home waters and an increasing demand for the commercially valuable halibut directed more and more attention to distant waters. In the first modern efforts to develop a fishery in more distant North Atlantic waters the means and methods of production in home waters were found wanting. Expeditions from Europe to Davis Strait were organized both in 1924 and 1925 but each failed due to factors that were not related to the availability of halibut. In 1926 and subsequent years properly organized and designed mothership expeditions and modern distant-waters fishing vessels achieved most successful results. It is unreasonable to assume that the stock of halibut suddenly developed in the area in 1926 coincident with the development of effective operational methods and of increased market demand.

Subsequent to the late 1920's the production of halibut in Greenland underwent the characteristic decline in response to relatively heavy removals. The same process has been repeated at Greenland since World War II as it has on all other European grounds.

North Pacific Halibut

A number of authors, particularly Ketchen (1956a) and Burkenroad (1948 and 1951), have contributed to the discussion upon the effects of natural forces upon the stocks and yields of the Pacific halibut. The question of natural fluctuations in the Pacific stocks and causes thereof have been a matter of concern and study by the International Pacific Halibut Commission since the start of its investigations over 30 years ago. The Commission practically pioneered the field of oceanic hydrographic studies in the northern waters of the North Pacific but the investigations were by necessity on a very limited scale (McEwen, Thompson and Van Cleve, 1930). An adequate study would have required annual funds many times in excess of those provided for all the work of the Commission.

Under an expanded program of research approved by the Commission in 1953, an intensive ten-year program of study of the sub-commercial sizes of halibut was commenced which may lead to some understanding of the complex factors underlying the relative success of recruitment. Such studies may provide clues to the influences that lead to the development of year-classes of varying strengths. Possible correlations between the success of halibut broods and the hydrographic environment will be continuously investigated. However, before such correlations

can have meaning, hydrographic observations will be required to be of a character that may be integrated both spatially and temporally with the life history of the halibut. It is hoped that the recent interest in North Pacific hydrography by various United States and Canadian oceanographic groups will, with the passage of years, fill the void existing in this field.

TEMPERATURE AND PRODUCTIVITY

Ketchen (1956a) concluded that there was a good visual correlation between the halibut catch per unit of effort data (in pounds) for grounds between Willapa Bay, Washington and Cape Spencer, Alaska (Area 2) and the smoothed air temperature trends at Masset, British Columbia 10 years earlier. The trend of catch per unit of effort data for stocks west of Cape Spencer (Area 3) also agreed in considerable detail with the mean annual air temperatures at Masset 12 years earlier (Fig. 4). It was thus felt that long-term environmental trends may have influenced the halibut stocks by the changed survival of young, and these trends could aid in the explanation of changes in catch per unit of effort that it was felt fishing alone could not do.

The catch per unit of effort statistics for the halibut were those developed by the International Pacific Halibut Commission. They may be considered to provide in general a reasonably satisfactory measure of abundance for the purpose at hand. Further refinement in the interest of improved comparability over the long term of the fishery are under study, but the obvious changes in the efficiency of the unit of effort have been provided for.

It has been shown that Masset temperature trends over the long term have not been representative of North Pacific temperatures. Furthermore, the use of fixed lags of 10 or 12 years for the halibut is subject to many limitations that impair the usefulness of the method. The presence of numerous age groups in the fishable stock tends to dampen or obscure the effects that year-classes below or above normal strength might otherwise have on the catch per unit of effort. Also, the technique makes no allowances for the considerable changes that have occurred from time to time in the fishing intensity which were probably accompanied by significant changes in the age composition of the stocks. For example, prior to 1920 the intensity was low and the stocks probably consisted of older fish on the average than during the period 1920–1930 when the intensity was much higher. Subsequent to 1931 the level of intensity was again changed due to regulation of the catch and the age composition undoubtedly adjusted to this new condition. In view of the probable changes in age composition, the large number of age groups in the stocks, plus the changes in growth rate observed in grounds west of Cape Spencer (Intern. Pacific Halibut Comm., Rept. No. 21), it is doubtful whether a fixed lag could correctly relate catch per unit of effort of adults to earlier environmental conditions regardless of their representativeness.

On the basis of the claims of Burkenroad (1948) that removals by the fishery on the western grounds were insufficient to account for the observed rapid decline in abundance between 1915 and the early 1920's (particularly between 1915 and 1918) and of the aforesaid resemblance in considerable detail between catch

per unit of effort and Masset temperatures, Ketchen stated that "the general downward trend in temperatures 10 to 15 years prior to the rapid decline in apparent abundance may have been responsible for decreased survival of young".

It is difficult to reconcile the aforementioned statement regarding downward trend of temperatures with the trend given for Masset. There was an upward trend in temperature at Masset, the station chosen by Ketchen to be related to the western halibut stocks, not a downward trend "10 to 15 years prior to the rapid decline in abundance" referred to. Both the annual and February–April Masset temperature trends increased from 1900 to 1907 in Ketchen's (1956a) figure 9, here reproduced as Figure 4, which period is "10 to 15 years prior" to the 1915 to 1918 sharp decline in catch per unit of effort of the halibut. Furthermore, San Francisco and New Westminster temperature trends, also portrayed in Ketchen's paper, were increasing or level and not declining during this period. Other Pacific Coast stations also show a rising trend of temperatures at this time (Fig. 5).

If, on the other hand, the sharp decline in catch per unit of effort from 1915 to 1918 was to be related to the sharp drop in Masset temperatures between 1907 and 1909, it would be necessary to assume that a significant portion of the western catches normally consisted of 8- to 9-year-old fish. Tabulations of early samples (Thompson, 1915) have indicated that such young age groups did not contribute significantly to the catches in those early years.

Ketchen also felt that the recovery of the Area 3 stocks between 1936 and 1944 was more rapid than expected and believed there was the possibility that more favourable (higher) temperatures in the winters between 1926 and 1936 led to an increased survival of young. While the observed good year-classes showing up in the catches of the mid-1940's may be attributed to such higher temperature levels, there were as many relatively poor year-classes produced during the same period of higher temperatures.

Recent developments in the fishery since 1952, while not covering many years and not fully allowing for the cushioning effect of old age groups on the catch, have indications of being inimical to the temperature hypothesis. The sharp decline in Masset air temperatures from 1942 to 1950, which in this instance is confirmed by all other coastal stations examined from San Francisco to Kodiak, should, according to the proposed hypothesis, result in a decline in the duly lagged catch per unit of effort starting about 1952 in Area 2 and in 1954 in Area 3. In Area 2 as a whole, the catch per unit of effort has been generally maintained in spite of sharp increases in the removals since 1950. In Area 3 there may be indications of a downward movement in the trend, but in this region also there has been a sharp increase in removals since 1951 that can account for any downward trend in catch per unit of effort. Thus developments in the fishery in both areas to date do not appear to support the hypothesis regarding the long-term relationship of catch per unit of effort and air temperature.

If a relationship between temperature and the abundance of halibut exists, over the long term it has been masked by the dominant effect of fishing. On the other hand, over the short term, depending upon the choice of data, both signifi-

cant and non-significant correlations have been currently observed. The complex and conflicting character of these relationships has demonstrated the inadequacies of available meteorological data and points out the lack of detailed knowledge regarding the incidence of mortality in the sub-commercial sizes of halibut. Also, as Gulland (1953) showed, when there is a wide choice of meteorological values available to relate with stock measures, there is a high probability of at least one good correlation between the two arising by chance alone.

NATURAL FLUCTUATIONS

Burkenroad (1948) felt that natural causes, perhaps of a regularly cyclical sort, were responsible for the major fluctuations in the halibut stock west of Cape Spencer. He believed the decline in stock size, as calculated from catch per unit of effort data from 1915 to 1918 in Area 3, could not be accounted for by the removals that had been made by the fleet in those four years. He also believed that the observed increase in catch per unit of effort during the period from 1930 to 1944 in Area 3 was much greater than could be accounted for by assuming a continuation of recruitment, growth and survival conditions that had shown, according to Burkenroad, "good agreement during the period from 1920 to 1929".

Applying the same methods of analysis to Area 2, and provided a fishing mortality of about 40 per cent was used, Burkenroad felt that the available data for that area did not reveal an impressive discrepancy between the catch and changes in abundance as they did after 1930 in Area 3. However, he believed that the available data were in error in that fishing mortality should have been 20 per cent in Area 2 instead of the 40 per cent determined by Thompson and Herrington (1930). It was felt that due to the non-migratory character of the Area 2 stocks and the fact that 96 per cent of the tagging reported by those authors was conducted in four (31 per cent) of the thirteen 60-mile sections in Area 2, and since these four sections yielded 63 per cent of the catch, the annual rate of fishing mortality amongst the tagged stocks may have been about three times that on the rest of Area 2 and nearly double that of Area 2 as a whole.

Several vital considerations appear to have been overlooked in coming to the above conclusions. With respect to the first conclusion regarding the 1915–1918 period in Area 3, the catch was then being taken from accumulated stocks in their primeval equilibrium state. Sharp and apparently disproportionate declines were inevitable as the compensatory build-up forces of growth and recruitment require time to become effective in a long-lived species whose population consists of survivors from many age-classes. Furthermore, the decline in catch per unit of effort or apparent stock size was further aggravated by the concentrated nature of the early fishery on the "discovery" spots and its restricted distribution as far as the total range of the stock was concerned. Similar abrupt and apparently anomalous declines have been observed in the early exploitation of many other fisheries, such as those for the Barents Sea plaice (Russell, 1942), Bear Island halibut (Devold, 1938) and Pacific blackcod (Bell and Pruter, 1954).

The second conclusion regarding the discrepancy between the actual and expected trends of stock size in Area 3 during the period 1930 to 1944 (Burkenroad, 1948, p. 110, fig. 5) was not surprising in view of that author's extrapolation of hypothetical recruitment, growth and survival values beyond the period for which they were established. Increases that have occurred in growth rate since 1930 (Intern. Pacific Halibut Comm., Rept. No. 21) largely remove the discrepancy between actual and expected levels of stock in Area 3 referred to by Burkenroad. Using the actual growth rates at various periods between 1930 and 1955 with the same values for fishing and natural mortality as used by Thompson and Bell (1934, p. 46, fig. 17) gives as good a correspondence between actual and theoretical catch per unit of effort as the latter authors found for the 1920 to 1929 period.

Burkenroad admitted that his third conclusion regarding the 20 per cent fishing mortality rate in Area 2 was based upon the questionable assumptions that (a) the area populated by halibut per linear 60-mile section off the coast averaged about the same in the four areas where most of the tagging was done as in the nine where little tagging was conducted, (b) the rate of addition to the stock per unit area populated averaged about the same in all thirteen areas and (c) the average density of fishable stock on the populated area in a sector was about proportional to the average catch per unit of effort there. Actually, charts available at the time show that the shelf area under 100 fathoms available to most demersal stocks, including halibut, varied widely from one 60-mile section of Area 2 to another (Table I). The four sections where most of the tagging was done contain approximately 43 per cent of the total 100-fathom or under grounds of Area 2 and about 49 per cent of the total area where actual fishing is conducted as shown by the log records of the fleet.

Thus, applying Burkenroad's same reasoning to published facts, it appears that tagging was done on grounds that would have contained at least 47 per cent of the fishable stock as determined by the sum of the products of the area under 100 fathoms and the 1929 catch per skate. The products of the area of the actual grounds fished (instead of the area under 100 fathoms) and the 1929 and 1930 catches per skate provided values of 51 and 55 per cent respectively in place of the foregoing 47 per cent. These same grounds produced 55 per cent of the Area 2 catch in 1929 and 56 per cent in 1930. In Table I the 1929 data are presented along with comparable but less precise 1928 data which were available to Burkenroad from reports of the Commission. The data for 1929 are used as it was the first year for which complete records of the bank of origin of the catches are available. Regardless of which year's data are used the general results are the same.

This indicated correspondence between yield and probable size of stock on the tagging areas invalidates Burkenroad's contention that Thompson and Herrington's fishing rate of 40 per cent was about twice what it should have been. With the validity of the 40 per cent fishing rate for Area 2 maintained, there can be little question of the dominant importance of fishery-induced changes upon the Area 2 stock. Also, the reasoning of Burkenroad (1951) based on the positive

TABLE I. Approximate area of grounds within the 100-fathom line in each of 13 60-mile halibut statistical Sections (Numbers 5–17 inclusive), and the catch and catch per skate in each for 1928 and 1929.

A: Approximate determination of the area within the 100-fathom line from U.S. Coast and Geodetic Survey charts numbers 7002 and 8002.

B and C: Data from Table 5, page 51, Thompson and Herrington (1930).

D: Product of the catch per skate and area within the 100-fathom line.

E and F: Data from International Pacific Halibut Commission files.

	A	B	1928 C	D	E	1929 F	G
Statistical Section No.	Area	Catch	Catch per skate	Product A×C	Catch	Catch per skate	Product A×F
	sq. mi.	10^3 *lb.*	*lb.*		10^3 *lb.*	*lb.*	
5	1380	242	43.1	59478	298	26.1	36018
6	1980	605	34.3	67914	722	28.5	56430
7	1800	312	34.3	61740	335	31.3	56340
8	660	390	34.3	22638	510	31.0	20460
9	1800	551	42.9	77220	980	30.8	55440
10	2630	3060	43.3	113879	2736	36.7	96521
11	2970	2345	51.7	153549	2775	41.8	124146
12	3330	2030	44.5	148185	1476	36.5	121545
13	3240	5188	51.1	165564	4748	38.8	125712
14	460	785	46.8	21528	1655	41.1	18906
15	1350	919	53.1	71685	2502	47.1	63585
16	1210	1283	54.0	65340	3266	44.0	53240
17	910	586	52.0	47320	1182	39.8	36218
Total of Sections 10, 11, 13 and 15	10190	11512	...	504677	12761	...	409964
Total, all Sections	23720	18296	...	1076040	23185	...	864561
Sections 10, 11, 13, 15 as % of total	43%	63%	...	47%	55%	...	47%

correlation between the catch per skate in Area 2 and in Area 3 from year to year that prejudiced the case for fishery-induced changes in the stocks in both areas, becomes in turn prejudicial to the case for naturally induced fluctuations in both areas.

Burkenroad also speculated, on admittedly weak evidence, on the possibility that the Area 3 halibut stock might rise rapidly for a few years after 1944 to double the 1933 level; and that, within the next half decade or so, that is about 1947 to 1952, the abundance might begin to drop precipitously, due to cyclical changes, despite restriction of the fishery. This pattern of cyclical stock changes in Area 3 suggested by Burkenroad has failed to materialize. In fact, there was some decline in the stock size from 1944 to 1949 with a subsequent increase to 1956 to levels higher than in the mid-1940's. Both trends were the reverse of Burkenroad's prediction despite the fact that the annual permitted catches were held at approximately stable levels.

Simpson (1956) observed that many fisheries show considerable fluctuations in yield but believed that some of the fluctuations can be ascribed to variations in the amount of fishing or changing effectiveness of various types of gear rather than to natural forces. He apparently incorrectly considered (p. 237) that the use of a standardized catch per unit of effort for the Pacific halibut stocks on the western grounds removes the effect of such man-made factors, thus appearing to infer that the historical changes in catch per unit of effort of halibut are indicative of natural fluctuations.

Beverton and Holt (1956) briefly reviewed the regulation of the Pacific halibut fishery, and they believed that in spite of the criticisms of Burkenroad the changes in catch and effort which have occurred since regulation was instituted, together with the previous history of the fishery, are too closely linked to be readily ascribable to natural fluctuations, but that commercial statistics of catch and effort alone are scarcely sufficient to give a conclusive answer. A further difficulty was noted by those authors, that even if it is accepted that recent trends in the fishery are due to regulation, it does not follow that the present state of the fishery is necessarily the best that could be obtained. As this latter question involves economic, political and social considerations it would be better treated elsewhere.

CONCLUSIONS

From the foregoing discussions it is evident that before satisfactory relationships can be established between climatological changes and the productivity of fish stocks, a great deal more must be known regarding both the environment and the fish themselves.

The effects of other variables such as economic conditions, changes in fishing practices and the extent of the removals by man should be accounted for. The possibility of fortuitous relationships must be discounted by exhaustive tests of the representativeness and adequacy of the environmental data, and equal care must be exercised in the selection and evaluation of the fishery data, particularly that of catch per unit of effort. Where the fishery data are defective

they should not be used to judge the effects of either the environment or man upon the stocks. Methodology of relating the variables, such as the time-lagging of data and the use of correlation analysis, must conform with the known facts about the species investigated.

With respect to the Pacific and Atlantic halibut, the effects of man's removals on the stocks appear to transcend any long-term effects that natural fluctuations may have had. The hypothesis that fishing, not natural forces, has been the major factor in affecting the stocks appears well founded.

ACKNOWLEDGMENTS

The authors are particularly grateful to W. E. Ricker, K. S. Ketchen, and a review committee of the Fisheries Research Board of Canada; R. Van Cleve and A. C. DeLacy of the College of Fisheries, University of Washington; O. E. Sette and F. C. Cleaver of the U. S. Fish and Wildlife Service; and D. G. Chapman of the University of Washington and statistical consultant to the International Pacific Halibut Commission, for their critical reading of the various drafts of this report and for both their agreements and disagreements with interpretations therein. The authors are also grateful to their colleagues, including the late Norman L. Freeman, on the staff of the International Pacific Halibut Commission who have provided data and editorial review.

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APPENDIX

Summaries of temperature data for the northwest coast of North America, and catches of Pacific cod in Alaska.

TABLE A. Mean annual air temperatures (°F.) at Tatoosh Island, Washington, at Ketchikan and Juneau, Alaska, and in "Southern Alaska". Sources: U.S. Weather Bureau, Annual Summaries for Washington and for Alaska Section.

Year	Tatoosh	Ketchikan	Juneau	"Southern Alaska"	Year	Tatoosh	Ketchikan	Juneau	"Southern Alaska"
1892	48.6	...	...	...	1925	49.4	45.6	42.1	41.4
1893	47.0	...	...	...	1926	51.4	46.9	45.6	44.7
1894	47.4	...	...	...	1927	48.6	43.7	41.3	40.5
1895	48.4	...	...	...	1928	49.5	45.6	43.0	41.3
1896	48.0	...	...	...	1929	48.4	44.4	42.9	41.5
1899	...	...	41.6	...	1930	48.6	46.2	41.7	40.3
1900	...	...	42.0	...	1931	50.2	47.4	43.5	41.9
1901	...	...	42.1	...	1932	51.1	45.7	40.6	39.4
1902	...	...	42.2	...	1933	48.0	44.6	39.4	38.9
1903	48.6	...	...	...	1934	51.1	47.9	43.4	42.2
1904	48.6	...	...	...	1935	49.1	45.7	41.1	41.4
1905	49.5	...	45.4	...	1936	49.6	46.6	42.2	41.9
1906	49.4	...	...	...	1937	49.0	46.0	42.6	42.0
1907	48.3	...	43.6	39.2	1938	49.3	46.8	43.0	41.6
1908	48.0	...	42.6	39.9	1939	49.6	46.3	42.5	40.9
1909	47.1	...	40.4	37.8	1940	51.5	48.1	44.0	43.0
1910	47.8	...	42.2	39.4	1941	51.6	47.6	44.2	43.0
1911	47.1	...	42.0	39.7	1942	50.0	47.6	44.0	42.2
1912	49.4	...	44.3	41.5	1943	49.4	46.0	43.4	41.5
1913	48.4	43.4	42.7	40.3	1944	49.7	47.2	44.8	42.6
1914	49.3	43.2	41.5	41.3	1945	48.6	45.6	42.1	41.4
1915	50.1	46.9	44.5	43.3	1946	48.7	45.4	42.2	41.0
1916	46.9	42.4	41.7	39.0	1947	50.1	46.1	43.0	41.6
1917	47.6	42.8	39.7	38.3	1948	48.4	46.6	41.2	40.0
1918	48.6	44.7	41.7	40.4	1949	48.2	46.2	41.3	40.3
1919	47.7	43.4	41.1	40.1	1950	47.1	44.8	40.3	...
1920	48.4	42.9	41.2	39.7	1951	48.1	45.5	41.2	...
1921	48.2	43.6	41.9	40.5	1952	48.4	46.0	42.8	...
1922	47.5	43.8	41.2	40.4	1953	50.2	46.9	...	...
1923	49.3	46.4	43.7	42.5	1954	49.3	45.8	42.8	...
1924	48.4	45.6	42.2	41.4	1955	...	43.6	41.0	...

TABLE B. Mean annual surface water temperatures (°F.) at Ketchikan, Alaska. Source: U.S. Coast and Geodetic Survey, 1952.

Year	Temperature	Year	Temperature	Year	Temperature
1922	46.7	1933	47.1	1943	...
1924	47.8	1934	47.9	1944	47.8
1925	48.0	1935	46.6	1945	47.8
1926	49.5	1936	47.1	1946	48.0
1927	48.5	1937	47.3	1947	47.5
1928	48.0	1938	47.7	1948	47.8
1929	48.4	1939	47.6	1949	47.1
1930	47.7	1940	49.3	1950	46.8
1931	49.0	1941	49.3	1951	47.4
1932	47.5	1942	48.8		

TABLE C. Mean "Seasonal" air temperatures (°F.) at Ketchikan, Alaska. Source: U.S. Weather Bureau, Annual Summaries for Alaska Section.

Year	January–March	April–June	July–September	October–December
1930	34.6	48.4	58.0	43.9
1931	40.6	51.0	57.3	40.5
1932	36.0	49.0	56.4	41.3
1933	35.9	48.9	56.1	37.6
1934	40.3	51.2	58.0	42.0
1935	35.2	47.9	57.1	42.6
1936	32.0	51.6	58.8	43.9
1937	34.7	49.7	56.9	42.9
1938	37.5	48.4	57.8	43.3
1939	37.1	48.1	55.8	44.3
1940	39.8	51.2	58.3	43.0
1941	39.2	51.0	58.1	42.0
1942	40.2	50.6	59.5	40.0
1943	35.2	48.6	55.5	44.8
1944	38.7	49.5	57.1	43.4
1945	38.7	48.5	55.3	39.6

TABLE D. Mean February–April air temperatures (°F.) at Sitka, Alaska. Source: U.S. Dept. of Commerce, Weather Bureau, Annual Summaries for Alaska Section.

Year	Temperature	Year	Temperature	Year	Temperature
1900	37.3	1906	39.4	1912	40.8
1901	37.2	1907	34.4	1913	38.5
1902	38.1	1908	37.0	1914	41.3
1903	35.8	1909	35.5	1915	42.1
1904	32.8	1910	36.0	1916	37.5
1905	41.1	1911	35.8	1917	36.9

TABLE E. Number of Bering Sea cod caught per vessel-ton, per-vessel-ton-per-day's absence from port, and per dory per season. Sources: Cobb, 1926, and *Pacific Fisherman*, various issues.

Year	Number per-ton-per-day's absence	Number per ton	Year	Number per-ton-per-day's absence	Number per ton	Thousands per dory
1882	1.45	380	1917	0.31	645	...
1883	0.67	497	1918	0.29	542	...
1884	1.39	604	1919	0.24	450	...
1885	1.24	497	1920	0.27	407	...
1886	2.19	565	1921	1.43	556	...
1887	5.68	670	1922	0.49	501	...
1888	2.42	650	1923	0.49	602	...
1890	4.62	522	1924	0.37	554	...
1891	1.21	532	1925	0.40	586	...
1892	0.63	553	1926	0.59	672	...
1893	1.70	456	1927	0.45	529	...
1894	1.03	469	1928	0.66	555	...
1895	1.16	471	1929	0.34	501	...
1896	0.56	400	1930	0.41	534	...
1897	0.56	398	1931	0.99	642	...
1898	1.25	356	1932	0.94	587	...
1899	0.64	494	1933	...	731	17
1900	0.58	477	1934	...	694	16
1901	0.53	456	1935	...	669	15
1902	0.53	540	1936	...	600	14
1903	0.47	546	1937	...	686	16
1904	0.72	565	1938	...	750	19
1905	0.34	581	1939	...	658	17
1906	0.46	581	1940	...	679	19
1907	0.53	565	1941	...	490	14
1908	0.30	549	1942	...	540	15
1909	0.45	642	1943	...	...	...
1910	0.39	556	1944	...	460	15
1911	0.42	623	1945	...	439	12
1912	0.54	525	1946	...	303	9
1913	0.43	549	1947	...	298	10
1914	0.25	565	1948	...	538	18
1915	0.27	617	1949	...	564	16
1916	0.31	686				

On the Preference of Roaches (*Leuciscus rutilus*) for Trinitrophenol, Studied with the Fluviarium Technique[1]

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ABSTRACT

The fluviarium, first described by Höglund (1951), has been improved in several respects.

The reaction of roaches in stepped concentration gradients of 2,4,6-trinitrophenol has been studied in the fluviarium; all gradients used were of 10 equal steps, the lowest step being always pure tapwater. Preliminary experiments showed that specimens of this species are attracted by this substance in concentrations lower than 3×10^{-4} molar. However, their responsiveness varies very much, and seems to depend on length as well as on age, the smaller fishes reacting more promptly than the larger ones, and the older fishes more promptly than the younger ones. These differences are probably caused by different activity of the fishes.

When the steepness of the gradients is increased the reaction of the fishes also increases, up to the gradient with maximal concentration about 8×10^{-5} molar. Then the reaction remains unaltered up to a maximum of at least 28×10^{-5} molar. Still steeper gradients cause a decrease in the reaction.

The weakest gradient causing a reaction of the roaches has been estimated by statistical extrapolation to be one with maximum concentration of 0.38×10^{-5} molar.

INTRODUCTION

Our present knowledge of the function and biological importance of the chemical senses of fishes is based almost exclusively upon observations made during the last sixty years. In 1895 v. Üxküll showed by experimental methods that organs of smell, as well as taste organs, co-operate in the search for food. Since then these sense functions have been studied extensively with the aid of training methods (for literature cf. K. Herter, 1953; Wunder, 1936; Moncrieff, 1951). Among other things, positive results were obtained as to the ability of fishes to discriminate the four taste qualities—sweet, sour, salt and bitter. Attempts were also made to estimate the threshold of discrimination of test substances corresponding to these four taste qualities in man, viz. cane sugar, lactic acid, sodium chloride and quinine. The low values of the threshold concentrations perceived by fishes indicate a very high sensitivity of the taste organs. Also the extreme acuity of the smell organs has been demonstrated by many authors. Probably these senses often play a rôle for the fishes when choosing location.

The present paper treats problems concerning the behaviour of fishes in concentration gradients of chemical substances. Obviously it is important for this kind of research to use an apparatus which gives the animals an opportunity of choosing a region within a reproducible and well defined concentration gradient. An apparatus furnishing such conditions was constructed by L. B.

[1]Received for publication October 20, 1957.

J. Fish. Res. Bd. Canada, 15(4), pp. 685–694, 1958.
Printed in Canada.

Höglund (1953) according to outlines advanced by the senior author of this communication. At first glance this method shows similarities to other gradient tank methods, introduced first by Shelford & Allee (1913), Wells (1915), and Erichsen-Jones (1947). However, great differences exist, which are discussed below.

As used for the present investigation the apparatus has been reconstructed in several respects (Fig. 1). The test substance studied by the present authors was 2,4,6-trinitrophenol. As is well known, this substance has a very bitter taste to man, perceptible in concentrations down to at least 0.4×10^{-5} molar.

IMPROVEMENTS OF THE FLUVIARIUM METHOD

The fluviarium method (Höglund, 1953) is based on the fact that a water mass, flowing without vortices, behaves as a rather stable system, i.e. a concentration gradient perpendicular to the direction of flow, once produced, will change comparatively little in a short time.

We are speaking here, like Höglund (l.c.), about gradients established in the trough. We are, however, actually not creating concentration gradients, but discontinuous changes or steps of concentration. Thus, by moving about in the test area or "yard", the fish pass one or more concentration steps. These concentration steps constitute stimuli, and it can be expected that the faster a fish moves through several such steps the greater is the stimulus to its chemical sense organs (cf. below). The form of the concentration steps used in the actual experiments is exemplified in Fig. 2 (maximal concentration 27.5×10^{-5} molar).

The original apparatus has been altered in the following respects. The "apportionment box" which causes an uneven distribution of kinetic energy through the asymmetrical arrangement of the inlets has been constructed in closer correspondence to hydrodynamic principles. It has been extended upstream into two symmetrical mouthpieces (Fig. 1) by means of which the water is introduced with streamlined turbulent flow into the two compartments of the "box". By this arrangement the stability of the gradient has been very much improved. The maximum variations in the different concentrations of the steps do not exceed 5%. The inlets of these mouthpieces have been provided with devices intended to reduce the turbulence already induced in the "fore jars" by the water jet. These devices are cylinders subdivided by a diaphragm with a circular hole, the latter being shielded off on either side with circular plates kept in position by spokes.

The former motor-driven stirrer has been replaced by a system in which mixing is effected by air bubbles rising from the bottom of the tank (Fig. 1: Stirrer).

It has been found that the form of the diaphragm-plate shown in Fig. 1 is more suitable than that of the pattern used by Höglund. In adopting the present shape of the plate the difference in flow-velocity between the surface- and bottom-currents in the two compartments of the box is taken into account.

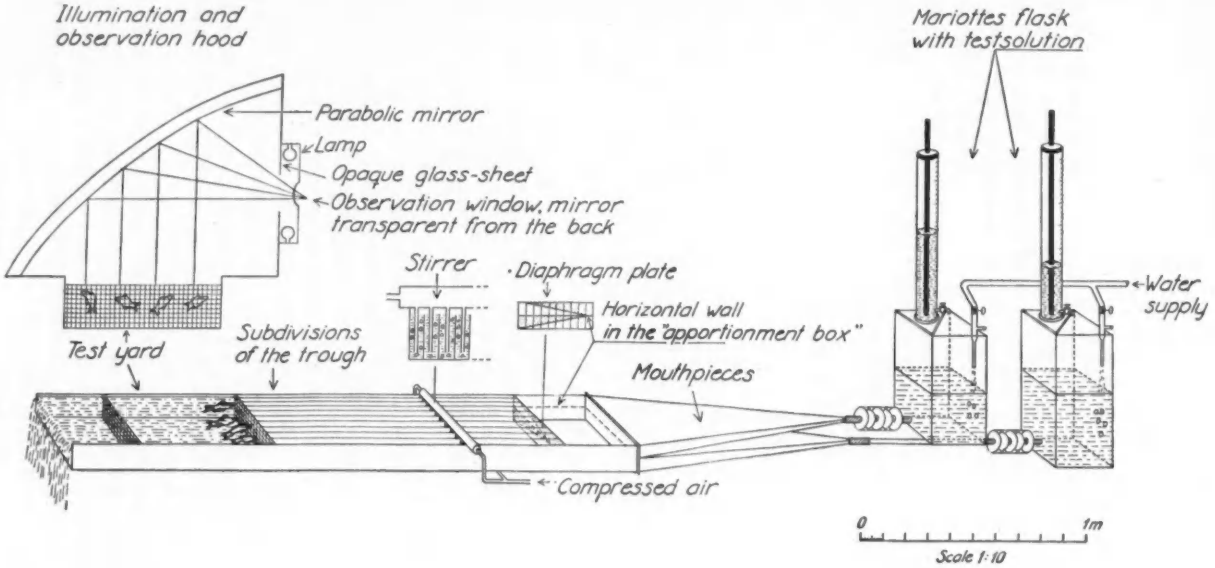

FIG. 1. General scheme of the fluvarium. The devices for observation, illuminating, and stirring are drawn in double scale.

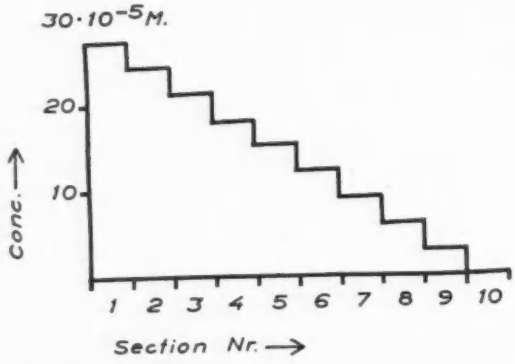

FIG. 2. Concentration gradient (steps) of 2,4,6-trinitrophenol, analysed by extinction measurements (353 mμ) with the Beckman spectrophotometer.

The observation hood was constructed so as to make it possible to record simultaneously the position of several fishes in the test area without errors caused by parallax. This is done with the aid of a parabolic mirror, which also serves the purpose of reflecting light from a shielded lamp on to the test area.

MATERIAL AND METHODS

In the experiments with 2,4,6-trinitrophenol to be described below, roaches (*Leuciscus rutilus L.*) have been used. These had been trapped in wire cages in Lake Mälaren.

In experiments in the fluviarium it is obviously necessary to use as test animals fishes sufficiently active so as not to be inclined to stay at the bottom when the rate of flow is very low. If this is nil, roaches move in the fluviarium spontaneously at about 2–3 cm/sec. at 7°C. At low flow rates they often orientate themselves perpendicularly to the direction of flow when swimming around in the test yard. It is thus rather difficult to define their position in relation to the gradient. By increasing the rate of flow it is, however, possible to induce a sufficiently strong rheotactic reaction. During the experiments described below the rate of flow was 2 cm./sec. The roaches were all the time at the upper grate of the test yard, swimming regularly from one side of the trough to the other with their bodies parallel or almost parallel to the direction of flow.

To get the fish accustomed to the new environment they were kept in the fluviarium for a week before the first experiment. Subsequently one experiment was performed on each day. As a rule the fishes do not spread quite symmetrically in the test yard, possibly on account of small differences in illumination or in the rate of flow in the vicinity of the walls of the test yard. Before each test a control experiment was therefore made without any test solution in the water. For about 5 minutes the position of each fish was noted every 30 seconds. This was done by dividing the bottom of the test yard into 10 sections, corresponding

to the subdivisions of the trough in front of the yard. After the control experiment the number of observed visits in every section, numbered successively 1–10, was added up. A frequency-curve of the visits in the respective sections was obtained (cf. Fig. 3), and an average value for the distribution, expressed by section number, was calculated. After the introduction of the test solution the same procedure of observation and calculation was applied as in the control experiment. As a measure of the the strength of the reaction the displacement of the average of the distribution was calculated, and the significance of the change examined using χ^2-analysis.

Blinded as well as unblinded animals were used in preliminary experiments. Blinding seemed to produce no advantage as the blinded animals stay close to the walls of the test yard. The blinding was accomplished by coagulating the lens and cornea by holding a red-hot nail close to the surface of their eyes. The injury was very slight, without any after effects. The fishes almost immediately regained condition.

Four minutes after the beginning of each experiment a water sample was taken, and the maximal concentration of the gradient determined with the aid of a Beckman spectrophotometer. The extinction was read at 353 mμ. In all experiments with trinitrophenol pH was regulated to that of the tap-water (viz. 7.3), by addition of NaOH. The water streaming through the fluviarium in these experiments was the tap-water of Uppsala. During the time of the experiment it had a temperature of 7–8°C.

EXPERIMENTS

Reaction Related to Size and Age

It may be stated at once that roaches seem to find 2,4,6-trinitrophenol pleasant, at least for rather short intervals of time; they react positively by swimming into higher concentrations. However, the strength of this reaction proved to vary very much between individuals. As such differences may influence the experimental results, it seemed important to search for its biological background. Thirty-four fishes were therefore tested one by one, in respect to their reaction to a gradient with a maximal concentration of 3×10^{-4} Molar trinitrophenol. In this manner they were divided into four groups, containing barely-reacting (No. 1) to strongly-reacting individuals (No. 4). The specimens were thereupon examined as to sex, length[2] and age (Table I). Estimation of the age was based upon scale-reading. The error of this method is discussed by Beckman (1943).

The dependence of the strength of the reaction to trinitrophenol upon the above mentioned characteristics has been statistically analysed (Table II). It appeared that the females were less influenced by the substance than the males, that older fishes were less influenced than younger ones, and that longer fishes were less influenced than shorter ones. Since the females in general were longer than the males, the difference in behaviour between the sexes might as well depend upon the difference in length.

[2]Length of fish was measured as "total" length with the tail in a normal position.

TABLE I. Length, sex and age of the roaches studied, classified as to their strength of reaction to trinitrophenol (group 1 – least reaction; group 4 – strongest reaction).

Group	Number of individuals	Length	Sex	Age
		cm.		*years*
1.	3	17.0	♀	6
	1	16.5	♂	7
	2	16.5	♀	6
	1	16.0	♀	6
	1	16.0	♀	5
	1	15.0	♀	6
	1	14.5	♂	5
	1	14.0	♀	4
2.	1	18.0	♀	7
	1	17.0	♂	7
	1	17.0	♂	6
	1	15.5	♂	6
	1	15.5	♀	6
	1	15.5	♀	5
	1	15.0	♀	4
	3	14.5	♀	4
	1	14.0	♂	5
	1	13.5	♂	5
	2	13.0	♂	4
	1	12.5	♀	3
3.	1	16.0	♂	7
	1	15.0	♂	6
	1	13.5	♀	5
	1	12.5	♂	4
4.	1	13.5	♂	5
	1	13.0	♂	5
	1	11.5	♂	4
	1	10.5	♂	3

TABLE II. Statistical treatment of data given in Table I. (This treatment was proposed by Dr. Eric Leander, to whom we express our sincere thanks.)

Linear regression model	Explanatory variables included	Residual sum of squares	Decrease in sum of squares: from model	to model	Decrease	Degs. of freedom	Mean squares	Variance ratio	P
A	–	30.97	–	–	–	33	0.94		
B	Length	18.12	–	–	–	32	0.57		
			A	B	12.85	1	12.85	22.7	<0.001
C	Sex	22.38	–	–	–	32	0.70		
			A	C	8.59	1	8.59	12.27	<0.001
D	Age	27.52	–	–	–	32	0.86		
			A	D	3.45	1	3.45	4.01	<0.05
E	Length, sex	15.27	–	–	–	31	0.49		
			B	E	2.85	1	2.85	5.8	<0.025
F	Length, age	14.34	–	–	–	31	0.46		
			B	F	3.78	1	3.78	8.2	<0.01
G	Age, length, sex	14.32	–	–	–	30	0.48		
			F	G	0.02	1	0.02	0.004	

When considering length and sex jointly, there is still a difference between the sexes with respect to the reaction. At a given length, females are somewhat less influenced by the substance. We obtain, however, a better fit when considering length and age as explanatory variables (Table II). The regression line for this approach is:

$$y = K - 0.63x_1 + 0.52x_2$$

(y strength of reaction in arbitrary units; K constant; x_1 length in cm.; x_2 age in years). In other words, for fishes of a given age, there is an average decrease in the intensity of reaction by 0.6 unit with an increase in length of 1 cm. On the other hand, considering fishes of a given length, there is an average increase in reaction by 0.5 unit with an increase in age of one year. In this case the total correlation coefficient is 0.73, as compared with 0.64 when sex and length are used jointly as explanatory variables. Furthermore, the dispersion (standard deviation) of the reaction related to age and length is much greater for males than for females. In the case of the latter the dispersion is rather small. None the less the fit is reasonably good due to the females falling quite well into the pattern outlined by the males.

When sex is introduced as a third explanatory variable, the fit is not appreciably improved (see Table II).

We are not able to explain the relationships demonstrated above. As the method used depends to a certain extent on the motions of the test animals, the more active individuals must experience a stronger sensation of the gradient than the less active ones. It is thus very probable that the observed difference in intensity of reaction between individuals reflects at least to some extent a difference in activity which should in some way be dependent on size and/or age. Poisoning effects of trinitrophenol must, however, also be considered. These problems will be treated later on the basis of further experiments.

Reaction to Gradients of Different Strengths

Our chief object was, however, to study the reaction of roaches in gradients of trinitrophenol of different strengths. A group of 6 or 7 fish with an average length of 10 cm. and an age of 3 years, were tested at the same time, and the same specimens were used throughout the whole series. These specimens never exhibited any tendency to school-behaviour, which must be considered as a necessary condition for statistical treatment of the single observations as outlined above.

The results from two experiments with very different strength of the reaction are illustrated in Fig. 3. When there is only a slight reaction (upper diagrams) the frequency-curves are still almost symmetrical. When the reaction is very pronounced, however, the frequency-curve is rather skew (Fig. 3, lower diagrams). In Table III we have given the displacements of the mean values of the distribution. The significance of the changes was estimated using the χ^2-test. In this way we find that with rising gradient the displacements become significant when the highest concentration in the gradient reaches 1.4×10^{-5} molar. A further increase

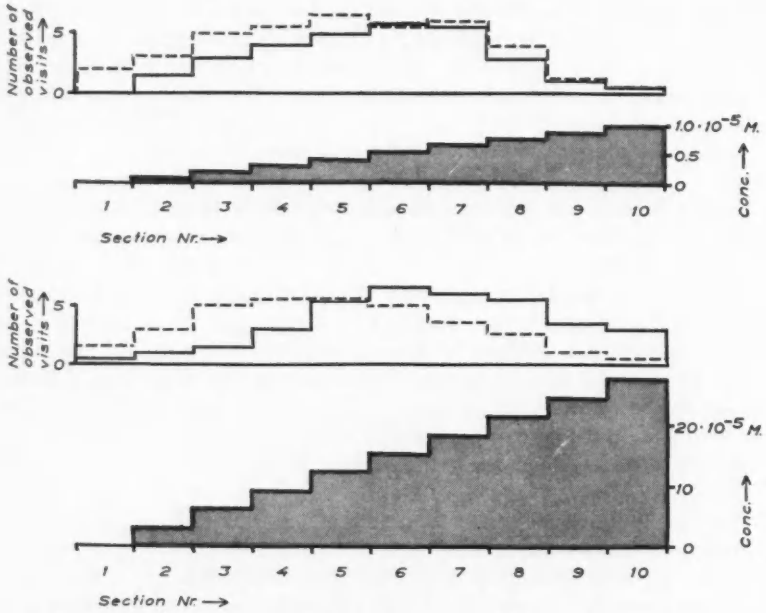

FIG. 3. Distribution of the fishes in relation to the 2,4,6-trinitrophenol gradient in an experiment with a high maximal concentration (above) and another with a low maximal concentration (below). *Abscissa*: Section numbers of the test yard. *Ordinate*: Frequency of observations and concentration of 2,4,6-trinitrophenol. The distributions of the fishes are given for the control experiment (broken lines) and for the test experiment (solid lines). The area indicating the trinitrophenol concentration is shaded.

of the steepness of the gradient makes the displacement somewhat greater. However, with a maximal concentration of the gradient from 8×10^{-5} to about 28×10^{-5} molar there is no further increase in the intensity of reaction of the fishes. Above this concentration the reaction declines. A comparison of the different control experiments reveals that rather small variations occur from day to day. Only between the two most extreme distributions out of 23 experiments is the difference significant ($\chi^2 = 18.03$, $P < 0.01$).

DISCUSSION

The observations recorded above indicate that the fish, when moving about in the test yard, prolong their stay in the higher concentrations of 2,4,6-trinitrophenol with increasing steepness of the gradient. Actually this is revealed also by direct observations. This might be a consequence either of the fishes preferring the water containing trinitrophenol to the pure medium, or a result of their activity being reduced by the trinitrophenol making them remain for longer periods of time in the higher part of the gradient. That the last mentioned

TABLE III. Reaction of roaches to 2,4,6-trinitrophenol in gradients of different steepnesses. Displacement is measured as the shift in mean position toward the higher concentrations, expressed as a fraction or multiple of a section of the gradient (10 sections were used; the lowest lacked trinitrophenol in all cases). Significance of displacement is estimated by χ^2-analysis.

Concentration in the highest part of the gradient	Displacement	Probability of occurrence by change
$\times 10^{-5}$ *molar*		P
0.36	0.08	0.95
0.41	−0.13	0.7
0.55	0.19	0.7
0.64	0.17	0.8
0.65	−0.25	0.7
0.68	0.58	0.01
0.87	0.61	0.3
0.90	0.51	0.1
0.94	0.64	0.01
0.97	0.43	0.7
1.1	0.65	0.02
1.4	0.88	0.001
1.9	1.22	0.001
2.9	1.34	0.001
3.5	1.24	0.001
7.8	1.51	0.001
22.6	1.56	0.001
27.5	1.59	0.001
52.6	0.92	0.02
106.0	1.03	0.001
118.0	0.62	0.01
120.0	0.95	0.001
348.0	0.22	0.9

explanation is not valid appears from the fact that the fishes at still steeper gradients do not accumulate in the part of the gradient having the higher concentration. Thus, above a certain concentration 2,4,6-trinitrophenol seems to be repellent to the fishes. In keeping with this view is the observation that, in gradients with maximal concentrations higher than 27.5×10^{-5} molar, the fishes come with increasing frequency to the surface of the water, making movements as if gasping for air. We interpret this as indicating that the animals are in some way disturbed.

In the lower concentration range there seems to be a fairly good correlation between the strength of the reaction and the concentration of 2,4,6-trinitrophenol (Fig. 4). Statistical treatment of all the determinations up to a concentration of 1.9×10^{-5} molar gives a correlation coefficient of 0.88 ($P < 0.0005$) with the regression line:

$$y = 0.85x - 0.33$$

where y is displacement and x is maximum concentration. This line intersects the abscissa at 0.38×10^{-5} molar. The gradient having maximal concentration 0.38, arrived at in this way, may be described as the lowest gradient perceived or preferred by the roaches used in the experiment.

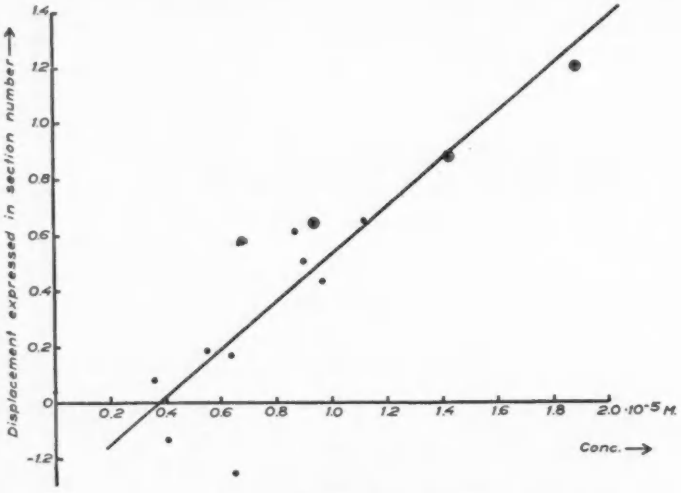

FIG. 4. Regression between the displacement of the mean of the distribution of the fishes in the test yard and the concentration of 2,4,6-trinitrophenol. Encircled points are statistically significant.

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Red Flesh in Redfish, *Sebastes marinus* (L.)[1]

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ABSTRACT

Occasional fillets of redfish salmon red in colour have been found in the Newfoundland area. A portion of a minced pair of the red fillets was extracted with acetone and the absorption spectrum of the solution measured at various wavelengths from 350 to 700 mμ. Maximum absorption was obtained at 475 mμ, which is similar to that of astaxanthin in acetone. An acetone extract of normal whitish-coloured redfish fillets showed no appreciable absorption over this range of wavelengths. Instances of red coloration of the flesh are also noted in haddock, cod and saithe.

INTRODUCTION

The brilliant colours of the skin, which are so characteristic of fishes, are largely due to the occurrence, within the dermal layers, of carotenoid and melanin pigments. The occurrence, distribution and biochemistry of the carotenoid pigments have recently been reviewed by several authors, notably Goodwin (1950, 1951, 1954) and Fox (1953). Generally the carotenoids are prominent in skin coloration but are not widely distributed in the muscle tissue of fishes.

A carotenoid was obtained from the pink muscle tissue of the Atlantic salmon, *Salmo salar* L., by Euler *et al.* (1933). This was later shown to be identical with astaxanthin by Emmerie *et al.* (1934).

Bailey (1937) obtained astaxanthin-like pigments from the flesh of sockeye salmon, *Oncorhynchus nerka* (Walbaum). Pigments from the flesh of steelhead trout, *Salmo gairdneri* Richardson, appeared to be similar to those obtained from the sockeye.

Sørensen and Stene (1938) found free unesterified astaxanthin in the muscles of sea-run and freshwater brown trout, *Salmo trutta* L. The sea trout entering the river from the sea possessed only about half the concentration of astaxanthin found in trout from Norwegian mountain lakes.

Steven (1948) has shown that astaxanthin is present in the flesh of *Salmo trutta* L. and of the char, *Salvelinus* sp., of Scottish lochs. This author remarks that it is obviously a widespread if not a general characteristic of the Salmonidae to store large amounts of astaxanthin in their muscles, probably as free astaxanthin. The amount of carotenoid pigment extracted from the body muscles of the brown trout was approximately proportional to the intensity of pigmentation of the flesh and none was obtained from trout with white muscle.

Although astaxanthin is not normally present in the flesh of cod, *Gadus callarias* L., a pink-fleshed cod has been reported, from Norwegian waters, containing astaxanthin in the muscle tissue (Baalsrud, 1956).

[1]Received for publication February 24, 1958.

J. Fish. Res. Bd. Canada, 15(4), pp. 695–700, 1958.
Printed in Canada.

Schmidt-Nielsen *et al.* (1932), while discussing the occurrence of astaxanthin in the liver of the lumpfish, *Cyclopterus lumpus* L., report that the flesh and milt of the males are pale red in the summer, during the spawning season.

RED FILLETS OF REDFISH

In June 1957 we received from C. M. Blackwood of the Fish Inspection Laboratory at St. John's, Nfld., the fillets of a redfish, *Sebastes marinus* (L.), which, instead of the normal whitish colour, possessed "red" flesh. This fish had been brought to the Laboratory from Ramea, on the south coast of Newfoundland, by the fisheries inspector in the area. The fillet was salmon pink in colour and resembled that of a salmon or sea-trout. The colour was not localized in any particular part of the fillet, but was evenly spread throughout the entire flesh.

Séguy's (1936) *Code universel des Couleurs* was consulted, and two observers, the junior author and Miss Dolores Bursey, agreed independently that the colour-index shade most nearly resembling that of the pink fillet was number 198 (salmon).

Spectrophotometric Analyses

In August 1957 we received four salmon-pink fillets from two redfish landed at the Isle aux Morts fresh fish plant on August 7, 1957, by the trawler *Zebu*. These fillets had been taken in the eastern part of the northern Anticosti Channel at 165 fathoms. From the appearance of the skin it was concluded that the redfish were of the *mentella* type, *Sebastes marinus mentella* Travin. These fillets were similar to the previous fillets from Ramea both in colour and texture.

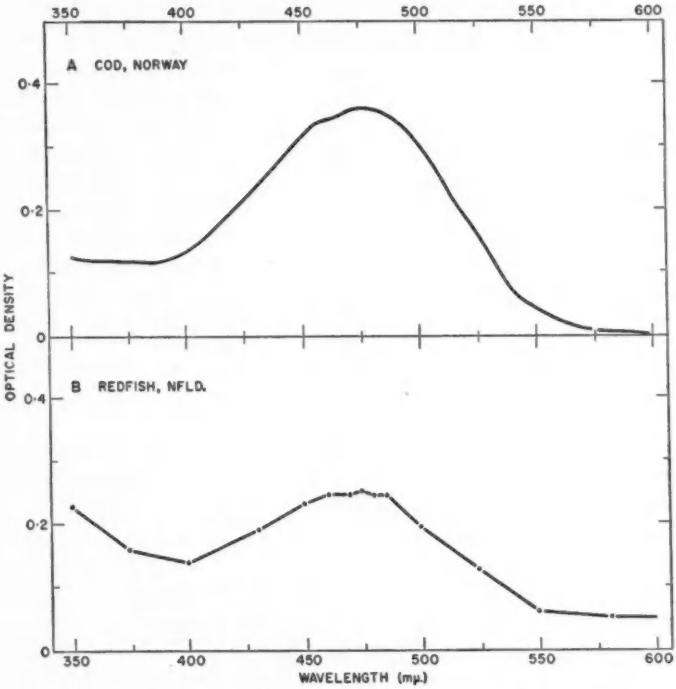
An analysis of the pink fillets was carried out by C. M. Blackwood at the Fish Inspection Laboratory. The four skinless redfish fillets were ground up and a 21-g. sample of mixed muscle extracted by shaking mechanically for 30 minutes with 100 ml. of acetone. The absorption spectrum of the solution was measured at various wavelengths from 350 to 700 mμ in a Beckman spectrophotometer.

The absorption curve B in the accompanying Figure resembles that of astaxanthin. For comparison an absorption curve, identified as resembling that of astaxanthin from an acetone extract of the flesh of a pink-fleshed cod (Baalsrud, 1956), is shown in curve A in the accompanying Figure.

Goodwin and Srisukh (1949) state that the absorption maximum of free astaxanthin in acetone is 475 mμ. The maximum in our data is also at this wavelength.

In December 1957, four skinless redfish fillets were taken from two redfish obtained by the research vessel *Investigator II* in experimental fishing off Cape St. George in the Gulf of St. Lawrence. These were normal, whitish-coloured fillets from the *Sebastes marinus mentella* variety of redfish, the common redfish of the Newfoundland area.

The fillets were minced and a 21-g. sample of each was extracted with 100 ml. of acetone in the same manner as were the red fillets. The optical density values for the acetone extracts from each of these normal fillets at wavelengths from 335 to 1000 mμ are shown in Table I. Absorption was negligible in the range



Absorption spectra of solutions of pigment (21 g. muscle tissue was extracted with 100 ml. acetone). A. Cod, *Gadus callarias* L., from Norway, after Baalsrud (1956). The absorption was measured in a 2-cm. cuvette. B. Redfish, *Sebastes marinus mentella* Travin, from Newfoundland. The absorption was measured in a 1-cm. cuvette.

400 to 700 mμ. It is evident that astaxanthin was not present in these normal white-coloured redfish fillets.

Chemical Analyses

Chemical analyses of the red and of the normal redfish fillets, gave the results shown in Table II.

Although the higher fat content of the red fillets may be significant, differences in chemical composition of the red and white fillets are not great, and the fat and protein composition of the red fillets can not at present be regarded as other than normal. If comparative chemical analyses could be carried out on a large number of specimens some real differences might be found.

D. L. Templeman, Fisheries Inspector, observed red-coloured flesh in a redfish of average size taken in the northern Gulf of St. Lawrence by a dragger and landed at Isle aux Morts several years ago. The outward appearance of this fish showed no unusual characteristics. L. A. Forward, a Fisheries Research Board

TABLE I. Optical density values of four normal redfish fillets. (21 g. of each fillet was extracted with 100 ml. acetone by shaking mechanically for 30 minutes. The extract was read in a Beckman spectrophotometer, using a 1-cm. cuvette.)

Wavelength	Optical density values			
$m\mu$				
335	...	.012	...	.018
340	.025	.050	...	.049
350	.035	.032	.014	.026
375	.018	.014	.009	.010
400	.006	.004	.003	.001
425	.003	.004	.003	...
450	.003	.004	.003	...
500	.003	.004	.003	.000
550	.001	.003	.002	...
600	.001	.002	.001	.000
625	.001	.002	.001	...
650	.001	.002	.001	...
700	.001	.002	.001	.001
800	.002	.003	.002	.002
900	.001	.001	.001	.001
910	.002	.002	.002	...
925	.004	.004	.004	.004
940	.011	.012	.012	...
950	.018	.019	.019	.019
1000	.028	.029	.031	.027

TABLE II. Analyses of red and normal redfish fillets.

	Composite sample from two red fillets	Composite sample from four normal white fillets	
	g.	g.	
Solids	24.9	20.6	per 100 g. wet muscle
Crude protein	18.3	17.4	" " " "
Fat (ethyl ether extract)	4.8	2.5	" " " "

technician, reports that at the fresh fish plant at Isle aux Morts a reddish-coloured fillet is occasionally found among the fillets of redfish landed from the Gulf of St. Lawrence.

The pigmented redfish fillets are not very plentiful; in tens of thousands of redfish fillets examined at the Biological Station from catches by research vessels and by local St. John's trawlers we have never seen a red fillet.

Fisheries Inspector D. L. Templeman states that in his association with the fresh and frozen fish industry during 14 years he has inspected many millions of pounds of fish, and that the red coloration of the flesh of groundfish is a very rare phenomenon.

OCCURRENCE OF ABNORMAL RED FLESH IN OTHER GROUNDFISH

Two haddock, *Melanogrammus aeglefinus* (L.), with pale red flesh were seen in the fresh fish plant at Fortune in 1955, probably in the spring, by fisheries officer G. Combden. The haddock, which were apparently from St. Pierre Bank,

possessed pigmented flesh resembling that of a salmon. The report is apparently reliable as the fisheries officer remembers remarking at the time that the fish appeared to be a cross between a haddock and a salmon.

A cod with flesh of a salmon pink colour was landed at Ramea on the south coast of Newfoundland during 1951–52 and was observed by Fisheries Inspector D. L. Templeman. This fish, caught in the inshore waters near Ramea, was about 20 inches (51 cm.) long and possessed a brownish skin colour which is characteristic of some shoal-water cod. It is not thought that the skin colour had any relation to the flesh colour, as Mr. Templeman has seen many thousands of pounds of these brown cod with normal flesh coloration.

Steinar Olsen (private communication, February 1958) says that during his researches on saithe, *Gadus virens* L., in Norwegian waters he has seen one saithe with red flesh.

DISCUSSION

It is possible that this unusual occurrence of astaxanthin in the fillets of redfish, haddock and cod is a pathological condition. Burkhardt *et al.* (1934) consider that the presence of astaxanthin in the occasionally red body oils of whales indicates a pathological condition. It has been shown that fishes do not synthesize astaxanthin, but derive this carotenoid from their diet (Goodwin, 1951, 1954, and Fox, 1953). Sources of astaxanthin in the diet of such fish are numerous, and euphausiids, copepods and shrimps will provide a source of astaxanthin (Goodwin, 1954). Euphausiids make up a considerable part of the diet of redfish in the Newfoundland area, and in the larger redfish it is presumably from euphausiids that much of the astaxanthin, which is the chief pigment of the redfish skin (Lederer, 1938), is obtained.

Astaxanthin already occurs in the skin of redfish, and the absorption from the gut of an unusually large amount of astaxanthin or a breakdown in the excretion of astaxanthin could lead to a condition whereby excess astaxanthin might be deposited in the muscle tissue.

The possibility exists that the unusual storage of astaxanthin in the flesh of such fishes, whether pathological or otherwise, is genetic in origin, and that if the centres of occurrence can be localized we may be presented with a further "biological tag". The occurrence, however, of these unusual specimens is probably too rare for this purpose.

ACKNOWLEDGMENTS

The authors are grateful to Mr. John P. Hennessey, Chief of the Department of Fisheries Fish Inspection Laboratory in St. John's and to Mr. C. M. Blackwood of the same laboratory for undertaking the analysis of the redfish fillets. Fisheries Inspectors G. Combden, J. Fudge, D. L. Templeman and L. Piercey, and Mr. S. Olsen and Mr. L. A. Forward of the St. John's Biological Station have also provided useful information.

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Grading Fish for Quality. 1. Trimethylamine Values of Fillets Cut from Graded Fish[1, 2]

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ABSTRACT

Whole and gutted cod and haddock were divided into three grades of quality by panels of plant foremen and experienced Department of Fisheries personnel. It was found that there was a close correlation between the degree of freshness, as judged by these men, and the trimethylamine values of the fillets cut from the fish. This correlation was less significant when the fish were graded by Department personnel inexperienced in handling and grading of fresh fish.

It would appear from these results that the trimethylamine value of cod and haddock muscle may be used with certain limitations, as an objective measure of spoilage in support of an organoleptic system of grading these fish.

INTRODUCTION

At the present time the Department of Fisheries of Canada is developing a system in which round or dressed fish, as they are being discharged from the vessels, will be graded for quality. This is part of a large program that was initiated on our Atlantic coast and which may ultimately include quality control and grading of all fresh and frozen Canadian fish products from the time they leave the vessels until they reach the consumer.

The Difficulties in Grading Fish for Quality

Those who are taking part in this work are fully cognizant of the difficulties of developing a program involving quality control and grading for fresh fish.

First there is the problem that arises from the wide variety of species of fishes caught for commercial purposes in Canada. There are at least 30 species of marine fishes, and about half as many species of freshwater fishes that must be taken into consideration. There appear to be many different spoilage patterns among these fish, suggesting that there may have to be a different set of standards for grading of each species, or at least for each group of closely related species.

The second difficulty lies in the definition of the term "quality" as applied to fish. Ordinarily, one thinks of quality as being synonymous with "freshness". Reduction in quality suggests that a certain amount of decomposition has taken place. Although the degree of decomposition brought about by bacteria and autolytic enzymes is very important, it is not the only factor to enter into the concept of quality.

Loss of quality can also result from physical maltreatment such as crushing,

[1]Received for publication February 26, 1958.

[2]Portions of the description of this work were included in a paper given at the F.A.O. Fish Processing Technologists Meeting, Rotterdam, Netherlands, June 25–29, 1956.

J. Fish. Res. Bd. Canada, 15(4), pp. 701–716, 1958.
Printed in Canada.

bruising, or faulty workmanship in cutting the fish. Some species have inherent characteristics that result in loss of quality quite apart from any post-mortem changes caused by enzymes. Examples of these are the peculiar odours that are associated with fish caught on certain of our fishing banks, also the softness that occurs in the muscle of some species and which, in part at least, is attributed to the metabolic changes and feeding habits associated with spawning. Among these and other factors determining quality, consideration must be given to the presence of parasites in the fish flesh.

There is also the difficulty that practically every system so far devised for grading fish under commercial conditions has been based on sensory assessments and human judgment. In the case of the personnel of a fish plant grading their own fish, and therefore willing to accept their own judgment, this may be satisfactory. But where a government intends to impose a system of grading on an industry on a national scale, the problem is not so simple. The industry itself has a right to be shown that the system of grading to be imposed on it will produce consistent results in the hands of a large group of government inspectors. No matter how cumbersome, it would be very desirable to have some method of checking the subjective grading by objective measurements of quality. From the evidence already on hand, it would appear that for the many species of commercial fishes to be tested, many different criteria for the objective measurement of quality may be required.

The very complexity of the problem of grading fresh fish indicates that it cannot be solved by developing any simple formula that will apply to all species of fishes in all parts of Canada. It must be done in terms of individual species or closely related groups.

This paper deals with cod, *Gadus (morrhua) callarias*, and haddock, *Melanogrammus aeglefinus*, caught in the waters off the Canadian Atlantic coast. For the sake of simplicity it restricts the use of the term "quality" to indicate that freshness which is gradually lost as decomposition of the fish takes place.

This work is concerned only with the quality of fish at the time they are being discharged from the vessel or shortly thereafter. If improperly cared for, these fish will deteriorate rapidly in the plant, during transportation, or in the wholesale or retail stores. This means that the grade given on the wharf may bear no relation to the quality of the fish by the time they reach the consumer. In order to have a relation between grades given on the wharf and retail quality, the fish must be held for limited periods of time under very rigid conditions of storage. However, this is not anticipated for the immediate future, and hence the chief purpose of this part of the grading program is to improve the quality of the landed fish.

Subjective Criteria of Quality

In practice the grading of fish on a commercial scale is, and will remain for some long time, an art and not a science. Basically it is nothing more than estimating the condition of the muscle beneath by examining the various changes that have taken place on the surfaces of the fish, including eyes, skin, gill area, and gut cavity (in the case of dressed fish). This may occasionally be supple-

mented by information obtained after cutting or breaking the fish and examining a portion of the muscle itself. The literature dealing with subjective grading of fish provides a variety of systems for observing and recording the visible changes that take place in the fish as they deteriorate. The methods range all the way from that of Love (1954) and Fazzina (1958) who attempt to correlate fish quality with the post-mortem changes occurring in the lenses of the eyes, to that of the very complex numerical scoring systems of Shewan *et al.* (1953) and Soudan *et al.* (1956), which take into account the appearance of the exterior of the fish as well as the odours, flavours, and texture of the muscle.

Our experience in attempting to grade fish organoleptically during the past several years has taught us several things:

(1) That a complex system of organoleptic examination of the fish as suggested by either Shewan or Soudan is a useful starting point for gaining general knowledge of the changes that take place as fish spoil.

(2) That fish do not always spoil in the same manner. Similar fish may spoil differently in different parts of the fish hold. They may spoil differently due to differences in the manner in which they have been cut or gutted on the deck, or iced in the hold. Whether they have been washed, gutted, or gilled will also affect the spoilage pattern. They may also spoil differently in different seasons of the year. And there is a slight difference in the spoilage patterns for large and small fish of the same species. This means that a grader must become accustomed to many modifications in the organoleptic spoilage pattern and acquainted with their significance in terms of the quality of the muscle beneath.

(3) In practice a grader must learn to work rapidly, with most of the judgment based on visual observation. Otherwise he could never keep up with the rate at which the fish are discharged from the vessels.

Judgment of Experienced Fish Plant Foremen

In some of our larger plants, there are men who have been concerned with fish quality for the greater part of their lives. These are the experienced foremen who are responsible for buying the fish from the fishermen and who oversee the processing of the fillets for the market. In some cases, they examine and grade the fish during discharge from the boats and they see the same fish when it is being filleted and packed. Their success as plant foremen is determined, to a considerable degree, by their ability to judge the quality of the fish they buy, and to send fish of the required good quality to a wide variety of different markets in the United States and Canada. It was through the help of these men that we learned many of the practical aspects of grading fish that cannot be obtained from textbooks or scientific papers. These same men also assisted in some of the early grading experiments recorded in this paper.

These plant foremen were told that the immediate aim of grading of the fish was to separate them into three categories:

Grade I. Fish from which good fresh fillets can be cut. These fillets are to be of a superior quality without any discoloration or off-odours.

Grade II. Fish which will produce fillets that are merchantable, but inferior to Grade I because of initial off-odours, slight discoloration, or softness.

Grade III. Fish that produce fillets with pronounced off-odours or discoloration, which should not be used in the fresh or frozen fish trade.

The division of the fish into these three grades by the foremen was based primarily upon the visible changes that have occurred in the eyes, gills, gut cavity and skin surface including the condition of the slime. This was frequently accompanied by noting firmness or elasticity of the muscles by pressure with the fingers.

In borderline cases, where there was some doubt about which grade the fish should be given, the visual observations were supplemented by noting the odours developing in the gills and gut cavity. Under laboratory conditions it was found that odours were very useful in determining the quality of the fish. In the vessel, on the wharf, or in the plant, there were obvious limitations to the use of odours, except where they were quite pronounced. It was frequently observed that laboratory-trained graders were more prone to use their sense of smell in examining the fish, while the experienced foremen relied almost solely on their senses of sight and touch.

Many attempts were made to produce a table summarizing the conditions of the gills, eyes, gut cavity, slime, and muscle texture corresponding to the three grades. This was fairly successful when applied to different lots of similar fish held under the same conditions and examined periodically. It was also useful in distinguishing the very fresh fish from the very stale fish. But the most difficult and important task of a grader is to distinguish fish that are approaching the borderlines separating the grades. Here it was found that such tabulated data were subject to continual modification. It was also found from bitter experience that men trained to grade fish by observing well controlled spoilage experiments in the pilot plant or in the laboratory were frequently very confused when confronted with fish in the plants or on the wharf. Months of practical experience in grading commercial fish are necessary before the grader becomes familiar with these variations.

Our immediate interest has not been to define the physical condition of the fish in the grades decided upon, or to describe the variations in the exterior spoilage pattern, but rather to determine whether there is any correlation between the quality of the fish as *judged by experienced graders* and by objective measurements made on the fillets cut from these fish.

There are many objective methods for assessing the quality of fish muscle. Those using the total volatile acids, total volatile bases, total volatile reducing substances, and trimethylamine content have each given satisfactory results in the hands of various workers. The trimethylamine content determination was chosen for this work because of the long experience we have had with it at this laboratory and because it has generally proved satisfactory as a measure of spoilage when applied to cod and haddock muscle.

EXPERIMENTAL PROCEDURES

The first fish to be graded organoleptically in these particular tests were placed in rows on long narrow tables in the pilot plant at this Station. Each indi-

vidual fish was graded as I, II, or III and a record was kept by the grader without discussion or communication with other graders.

Particular care was taken to get miscellaneous lots of fish for these tests. Each lot included shore-caught and trawler-caught fish, gutted and ungutted fish, gilled and ungilled fish, fish that had been well iced and fish that had been poorly iced or not iced at all; included were fish that had been stored in ice for 1 to 14 days.

Immediately after the grading had been completed, the fish were filleted and the trimethylamine values[3] of the fillets were determined, according to the method used by Dyer (1945, 1950).

Usually 4, 6, or 8 men graded each lot of fish. Although the individual grades were recorded, the final results are in terms of the judgment of the group as a whole. This was done in the following manner. If 6, 7, or 8 out of 8 men agreed on a grade for a given fish, that grade was accepted and recorded. Where there was a more pronounced division of opinion the grades were recorded as "I or II" or "II or III". The incidence of opinions which lead to the "assigned grade" of the fish was also recorded.

EXPERIMENTAL RESULTS

Tests with Experienced Graders

The first test was carried out by 8 experienced plant foremen grading 150 mixed cod and haddock. The results are shown in Tables I, II, and III.

Table I. TMA values of 150 fillets cut from cod and haddock that had been graded by a panel of 8 experienced plant foremen.

Number of fish graded	Grading record for panel of eight			Assigned grade	Average TMA value		Number of fish per assigned grade
	I	II	III		Per batch	Per assigned grade	
63	8	0	0		0.39		
14	7	1	0	I	0.74	0.47	84
7	6	2	0		0.64		
1	5	3	0		0.22		
1	5	2	1	I or II	2.40	0.83	5
2	4	4	0		0.30		
1	3	5	0		0.92		
5	2	6	0		3.17		
1	2	5	1		3.80		
4	1	7	0		1.90		
4	1	6	1		1.89		
5	0	8	0	II	4.42	3.34	26
2	0	7	1		6.50		
3	0	6	2		4.45		
2	1	4	3		1.73		
1	1	3	4		1.28		
1	0	5	3		2.40		
4	0	4	4	II or III	8.30	7.10	11
5	0	3	5		8.24		
8	0	2	6		9.44		
5	0	1	7	III	11.02	12.04	24
11	0	0	8		14.40		

[3]The term "trimethylamine value", for which the symbol "TMA value" will be used, denotes milligrams of trimethylamine nitrogen per 100 g. of muscle.

TABLE II. Frequency distribution of TMA values for 150 fillets cut from cod and haddock that had been graded by a panel of 8 experienced foremen.

No. of fish graded	Grading record for panel of 8			Frequency distribution of TMA values (number of fish)														
	I	II	III	0–.2	.21–.4	.41–.6	.61–.8	.81–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	Over 10
63	8	0	0	26	15	12	3	2	4	1	–	–	–	–	–	–	–	–
14	7	1	0	4	3	1	2	–	3	1	–	–	–	–	–	–	–	–
7	6	2	0	1	2	2	–	1	1	–	–	–	–	–	–	–	–	–
1	5	3	0	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
1	5	2	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
2	4	4	0	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–
1	3	5	0	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
5	2	6	0	–	–	–	–	–	3	–	–	1	–	1	–	–	–	–
1	2	5	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
4	1	7	0	–	–	–	1	–	2	–	–	1	–	–	–	–	–	–
4	1	6	1	–	–	–	–	–	2	2	–	–	–	–	–	–	–	–
5	0	8	0	–	–	–	–	1	1	–	1	1	–	–	–	–	–	1
2	0	7	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1
3	0	6	2	–	–	–	–	–	1	–	–	1	–	–	1	–	–	–
2	1	4	3	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–
1	1	3	4	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
1	0	5	3	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
4	0	4	4	–	–	–	–	–	–	–	1	–	–	–	1	–	1	1
5	0	3	5	–	–	–	–	–	–	–	–	1	–	1	1	–	–	2
8	0	2	6	–	–	–	–	–	1	1	–	–	–	–	2	–	–	4
5	0	1	7	–	–	–	–	–	–	–	–	–	–	–	1	1	–	3
11	0	0	8	–	–	–	–	–	–	–	–	–	–	–	–	1	–	10

TABLE III. Frequency distribution of TMA values for 150 fillets cut from cod and haddock which had been graded by a panel of 8 experienced plant foremen.

Assigned grade	Number of fish	Frequency distribution of 3 TMA levels		
		0–1	1–5	Over 5
		%	%	%
I	84	88	12	0
I or II	5	40	60	0
II	26	8	77	15
II or III	11	0	36	64
III	24	0	8	92

The data are arranged in decreasing order of the grades assigned to the fish by the panel of 8 men. It may be seen (Table I) that the average TMA values increased as the quality, as indicated by the grades, decreased. Average values can sometimes be misleading; therefore, in Table II the average TMA values have been replaced by the number of fish of each grade that fell into 15 classes with TMA levels between 0 and "more than 10". The data from Tables I and II are consolidated in Table III.

Together the data in Tables I, II and III bring out the following points:

(1) There is a general agreement among the graders on the quality of the individual fish. With 58% of the fish there was complete agreement among all 8 men. With 69% of the fish, 7 or 8 of the 8 men agreed; with only 13% of the fish was there a marked division of opinion as to the grade in which the fish should be placed.

(2) There appears to be a significant correlation between the TMA values and the grades given to the fish by the foremen.

In the second test, 200 fish were graded by 8 Departmental personnel, chosen as the most experienced in handling and grading fresh fish. The results of these gradings are shown in Tables IV to VI. The results are much the same as those obtained by the plant foremen. Once again it is shown that the quality of the fish as indicated by this panel of graders is correlated with the TMA values.

TABLE IV. TMA values of 200 fillets cut from cod and haddock that had been graded by a panel of 8 experienced fishery officers.

Number of fish graded	Grading record for panel of eight			Assigned grade	Average TMA value		Number of fish per assigned grade
	I	II	III		Per batch	Per assigned grade	
7	8	0	0		0.4		
25	7	1	0	I	0.5	0.53	41
9	6	2	0		0.7		
7	5	3	0		0.9		
10	4	4	0	I or II	1.0	1.54	34
2	4	3	1		1.9		
15	3	5	0		1.5		
2	3	4	1		2.3		
13	2	6	0		1.6		
6	2	5	1		2.7		
16	1	7	0		3.4		
4	1	6	1		2.9		
5	0	8	0	II	2.4	2.73	71
10	0	7	1		2.0		
3	1	5	2		1.2		
2	1	4	3		4.8		
10	0	6	2		4.1		
14	0	5	3		5.6		
1	1	2	5		1.4		
10	0	4	4	II or III	4.1	4.88	35
10	0	3	5		5.0		
6	0	2	6		8.2		
5	0	1	7	III	15.7	13.2	19
8	0	0	8		15.3		

The third test was made with a panel of the four most experienced fresh-fish inspectors, grading a group of 250 fish. The results, summarized in Tables VII to IX are a repetition of the previous results.

Similar tests were repeated throughout the year and in every case the results were approximately the same: 85 to 95% of the fish assigned grade I by the panels of graders had TMA values of 0 to 1; 85 to 95% of the fish graded III had TMA values over 5; and about 75% of the fish graded II had values between 1 and 5.

TABLE V. Frequency distribution of TMA values for 200 fillets cut from cod and haddock that had been graded by a panel of 8 experienced fishery officers.

No. of fish graded	Grading record for panel of 8			Frequency distribution of TMA values (number of fish)														
	I	II	III	0–.2	.21–.4	.41–.6	.61–.8	.81–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	Over 10
7	8	0	0	3	–	3	1	–	–	–	–	–	–	–	–	–	–	–
25	7	1	0	9	5	6	3	1	1	–	–	–	–	–	–	–	–	–
9	6	2	0	2	–	3	1	–	3	–	–	–	–	–	–	–	–	–
7	5	3	0	–	1	1	1	2	2	–	–	–	–	–	–	–	–	–
10	4	4	0	–	1	1	–	3	5	–	–	–	–	–	–	–	–	–
2	4	3	1	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–
15	3	5	0	1	–	–	1	3	7	1	2	–	–	–	–	–	–	–
2	3	4	1	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–
13	2	6	0	–	–	1	3	1	6	1	–	1	–	–	–	–	–	–
6	2	5	1	–	–	1	1	–	–	2	1	–	–	1	–	–	–	–
16	1	7	0	–	–	–	1	1	5	2	2	2	–	1	–	1	–	1
4	1	6	1	–	–	–	–	–	2	1	–	–	–	1	–	–	–	–
5	0	8	0	–	–	–	–	1	1	2	–	1	–	–	–	–	–	–
10	0	7	1	–	–	–	1	–	5	2	1	–	1	–	–	–	–	–
3	1	5	2	–	–	–	–	1	2	–	–	–	–	–	–	–	–	–
2	1	4	3	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–
10	0	6	2	–	–	–	–	2	2	1	1	–	1	–	2	–	1	–
14	0	5	3	–	–	–	–	–	2	3	4	–	–	1	–	–	1	3
1	1	2	5	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
10	0	4	4	–	–	–	–	–	4	2	1	1	–	–	–	–	–	2
10	0	3	5	–	–	–	–	–	1	5	–	–	1	–	–	1	–	2
6	0	2	6	–	–	–	–	–	–	–	–	–	2	1	1	–	–	2
5	0	1	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
8	0	0	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8

TABLE VI. Frequency distribution of TMA values for 200 fillets cut from cod and haddock that had been graded by a panel of 8 experienced fishery officers.

Assigned grade	Number of fish	Frequency distribution of TMA values		
		0–1	1–5	Over 5
		%	%	%
I	41	90	10	0
I or II	37	44	56	0
II	71	21	63	16
II or III	35	0	69	31
III	19	0	0	100

TABLE VII. TMA values of 250 fillets cut from cod and haddock that had been graded by a panel of 4 experienced fishery officers.

No. of fish graded	Grading record for panel of four			Assigned grade	Average TMA value		No. of fish per assigned grade
	I	II	III		Per batch	Per assigned grade	
55	4	0	0	I	0.52	0.57	66
11	3	1	0		0.80		
19	2	2	0	I or II	1.25	1.25	19
20	1	3	0	II	1.50	3.27	74
37	0	4	0		2.44		
4	1	2	1		4.51		
13	0	3	1		7.98		
21	0	2	2	II or III	7.23	7.23	21
14	0	1	3	III	9.29	11.01	70
56	0	0	4		13.08		

TESTS WITH INEXPERIENCED GRADERS

It must be emphasized that in the tests described above, every effort had been made to obtain foremen or graders who had had long experience in judging the quality of cod and haddock. For comparison we were interested to learn what the results would be with a panel of men who were less familiar with fresh fish.

To do this, a comparison was made, using two different groups of fishery inspectors. The first group consisted of the most experienced fresh-fish men; the second were men familiar with dried and salted fish, who had little or no occasion to judge fresh fish. Both groups graded the same lot of cod and haddock. Table X gives a summary of the results. A better correlation between the group judgment of the more experienced graders and TMA values is found than is evident from the results obtained by the inexperienced graders.

GRADING FISH IN THE PLANTS

Up to this point, all fish used in the tests had been purposely selected so as to provide a wide assortment of quality and each fish was graded individually. In actual practice graders would not have to deal with such wide variations of quality within small lots of fish, and they would grade fish in batches, not individually.

In the following tests, the locale of the grading was changed from the pilot plant to a commercial fish plant. Three different types of tests were made:

(1) The graders were asked to select typical fish for each grade from boxes in transport from the boat to the cutting line; doing this, they ignored fish of borderline quality.

(2) They were also asked to grade individual fish selected at random from the cutting line by someone else. In this case most of the poorer fish had already been discarded by the plant operators and the chief problem was to separate grades I and II.

TABLE VIII. Frequency distribution of TMA values for 250 fillets cut from cod and haddock that had been graded by a panel of 4 experienced fishery officers.

No. of fish graded	Grading record for panel of 4	Frequency distribution of TMA values (number of fish)														
	I II III	0–.2	.21–.4	.41–.6	.61–.8	.81–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	Over 10
55	4 0 0	12	13	12	9	6	3	–	–	–	–	–	–	–	–	–
11	3 1 0	2	3	1	2	1	1	–	1	–	–	–	–	–	–	–
19	2 2 0	–	–	4	2	2	9	2	–	–	–	–	–	–	–	–
20	1 3 0	–	–	–	1	4	12	3	–	–	–	–	–	–	–	–
37	0 4 0	–	–	–	2	2	14	9	2	6	1	1	–	–	–	1
4	1 2 1	–	–	–	–	–	1	1	1	–	–	–	–	–	–	6
13	0 3 1	–	–	–	–	–	1	2	1	2	–	–	–	–	–	
21	0 2 2	–	–	–	–	–	1	1	2	4	3	1	–	3	1	5
14	0 1 3	–	–	–	–	–	–	–	1	2	2	1	1	1	–	–
56	0 0 4	–	–	–	–	–	–	–	–	–	4	1	1	1	1	48

TABLE IX. Frequency distribution of TMA values for 250 fillets cut from 250 cod and haddock that had been graded by a panel of 4 experienced fishery officers.

Assigned grade	No. of fish	Frequency distribution of 3 TMA levels		
		0–1	1–5	Over 5
		%	%	%
I	66	92	8	0
I or II	19	42	58	0
II	74	12	75	13
II or III	21	0	38	62
III	70	0	5	95

TABLE X. Frequency distribution of TMA values for 200 fillets cut from cod and haddock that had been graded separately by a panel of 2 experienced fresh-fish inspectors and 2 inexperienced fishery officers.

Assigned grades	Number of fish	Frequency distribution of TMA values			Number of fish	Frequency distribution of TMA values		
		Experienced graders				Inexperienced graders		
		0–1	1–5	Over 5		0–1	1–5	Over 5
		%	%	%		%	%	%
I	50	92	8	0	56	55	38	7
I or II	38	37	63	0	45	33	47	20
II	40	10	80	10	59	23	57	20
II or III	31	9	61	30	29	21	38	41
III	31	0	13	87	11	18	36	46

(3) The graders were asked to assess the quality of fish in batches of large boxes as they were being discharged from the vessel. Each box held about 500 lb. of fish.

TMA values were determined on a fillet of each of the fish that had been individually graded. From a batch of fish in a box, 6 to 8 samples were taken and their TMA values determined.

GRADING INDIVIDUAL FISH

Table XI gives the results of selecting typical fish of each grade. The greatest difficulty was in finding grade III fish, because most of the poorer fish had been previously eliminated by the plants. This probably accounts for the very low average TMA values for grade III fish. There were certain specific instances where the results were not so decisive as the examples given. This occurred with "bilgy" fish and "ping-pong" haddock (these are very small haddock, not gutted at sea, and frequently handled less carefully than the remainder of the catch).

TABLE XI. TMA values of fish selected in two different commercial plants as being typically grade I, II, and III.

Fish No.	Grade	In plant A		In plant B	
1		0.5		0.85	
2		0.3		0.64	
3		0.9		0.62	
4	I	0.5	average 0.59	0.73	average 0.68
5		0.5		0.58	
6		0.6		0.66	
7		0.4		0.52	
8		0.7		0.89	
9		2.2		3.8	
10		1.1		3.3	
11		3.6		4.5	
12	II	4.4	average 3.1	4.2	average 3.2
13		3.4		2.6	
14		3.7		3.4	
15		4.7		1.2	
16		1.3		2.6	
17		6.4		5.6	
18		5.2		6.8	
19		6.4		6.5	
20	III	5.8	average 6.8	4.9	average 5.6
21		11.6		8.3	
22		8.2		4.0	
23		5.0		2.6	
24		5.5		6.0	

Where a series of individual fish was graded in the commercial plant, the results were much the same as those previously obtained in the pilot plant, except that there were fewer grade III fish. For example, 100 fish ranging in TMA values from 0.05 to 9.6 were handed to one experienced fishery officer for grading. He rapidly divided them into 66 grade I, 34 grade II, and assigned none to grade III. Of the 66 fish of grade I, 62 had TMA values between 0 and 1.0 and 4 had values between 1.0 and 4.0. Of the 34 fish graded II, 24 had values between 1.0 and 5.0, 6 were below 1.0 and 4 were over 5.0. By changing these figures to percentages, we get the information in a form comparable with that of Tables III, VI, IX, and X:

Grade	*No. of fish*	*TMA 0–1*	*TMA 1.1–5*	*TMA over 5*
I	66	95%	6%	0%
II	34	18%	70%	12%

GRADING BOX-LOTS OF FISH

Thirty-eight large boxes of gutted cod or haddock were graded by one experienced Departmental inspector shortly after they had been discharged from the trawlers. These particular fish were to be cut and shipped as fresh, unfrozen fillets to central Canada and were supposed to have been of relatively high quality. Table XII shows in ascending order grades given and the average TMA

TABLE XII. TMA values for 38 boxes of fish, graded in the plant. The TMA values recorded are from 6 to 8 fish taken from each of the boxes. The figures within each grade have been arranged in order of increasing average TMA values.

Lot Number	Grade	Average TMA value	Range of TMA values
1	I	0.1	0.1–0.2
2	I	0.2	0.1–0.3
3	I	0.2	0.1–0.2
4	I	0.2	0.1–0.4
5	I	0.2	0.1–0.2
6	I	0.2	0.1–0.3
7	I	0.2	0.1–0.3
8	I	0.2	0.1–0.3
9	I	0.2	0.2–0.2
10	I	0.2	0.1–0.2
11	I	0.3	0.1–0.4
12	I	0.3	0.2–0.4
13	I	0.3	0.2–0.4
14	I	0.3	0.2–0.4
15	I	0.3	0.2–0.5
16	I	0.4	0.3–0.6
17	I	0.4	0.3–0.5
18	I	0.4	0.2–0.5
19	I	0.5	0.3–0.8
20	I	0.5	0.4–0.6
21	I	0.6	0.2–0.9
22	I	0.6	0.3–0.9
23	I	0.7	0.4–1.0
24	I	0.8	0.5–1.1
25	I	1.6	0.5–3.0
26	II	1.5	1.2–2.0
27	II	0.9	0.4–1.2
28	II	1.0	0.7–1.5
29	II	1.8	1.0–2.2
30	II	1.8	0.6–3.2
31	II	2.1	1.4–2.9
32	II	2.3	1.6–2.7
33	II	2.7	2.4–3.1
34	II	3.1	1.9–4.1
35	II	3.6	1.5–5.8
36	II	3.8	1.3–7.0
37	II	4.2	2.5–5.7
38	II	5.2	1.0–11.0

values. In only one instance did the grader show some hesitation in deciding on the grade.

It may be seen once again that the TMA values for fish graded I almost completely fall between the levels of 0.0 and 1.0, and those graded II are between 1.0 and 5.0. It is unfortunate that poorer quality fish, to indicate the borderline values between grades II and III under these conditions, were not encountered in these tests.

In Table XIII there is a similar set of data for grade III fish only. In each instance, these fish had been accepted by certain plants as "poor quality but still fit for consumption". In each case also, an experienced grader judged the fish as grade III, with the general comment "These are the type of fish we would like to keep off the market."

TABLE XIII. TMA values of 11 lots of fish condemned as grade III by an experienced fresh-fish grader, but which were going to be cut by the plants as "poor quality but still edible". The TMA values are based on 8 fish taken from each lot.

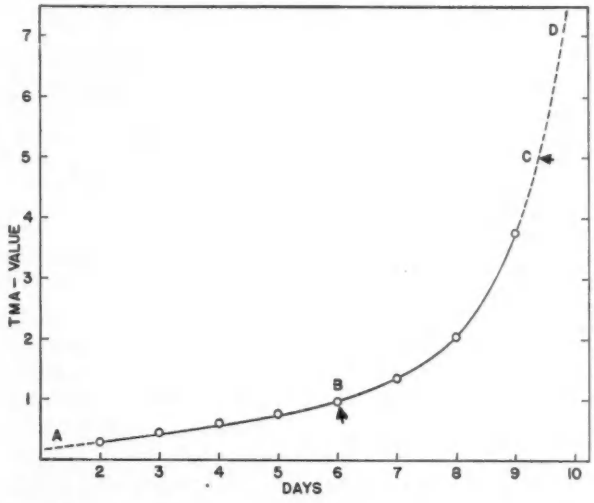
Lot No.	Species	TMA-value		Grader's comment
		Average	Range	
1	Cod	7.29	2.1–13.8	Very sour
2	Cod	3.57	1.2– 9.4	Mixed quality—might pass as poor seconds
3	Cod	5.67	2.6– 8.3	Sour
4	Cod	6.82	2.3–10.6	Sour
5	Haddock	8.15	5.7–11.8	Sour
6	Haddock	10.7	6.7–14.3	Sour
7	Haddock	23.1	11.2–39.0	Rotten
8	Haddock	7.74	2.9–13.8	Bilgy and sour
9	Haddock	5.27	2.1– 8.7	Bilgy and sour
10	Haddock	2.52	1.8– 3.5	Ungutted small haddock—faecal
11	Haddock	5.58	0.7–10.3	Ungutted small haddock—faecal

DISCUSSION AND CONCLUSIONS

If we accept the judgment of these experienced plant foremen and fishery personnel regarding the quality of fish, then it would appear that the TMA value might be used as an objective measurement of quality of dressed or gutted cod or haddock. TMA values between 0 and 1 indicate fish judged by these men to be of prime quality; values between 1 and 5 indicate fish that are spoiling, but still capable of producing merchantable fillets; where the value exceeds 5, the fish have reached a condition that is considered unfit for processing as fresh or frozen fillets.

In considering these results it must be borne in mind that subjective judgments of quality are quite arbitrary. What is considered as "fresh", "merchantable" or "edible" depends entirely upon the experience and point of view of the person making the judgment. This becomes very obvious when we begin comparing the standards of quality in various fish-producing countries and even in different regions within the same country. Fish that are condemned as "unmerchantable" or "unfit for human consumption" in one country, are readily accepted in another. All descriptive terms dealing with the quality or degree of freshness of unprocessed fish frequently need to be re-defined when used in another geographical area. For example, in discussing the quality of fresh fish with the authorities of a large city on the Atlantic coast of the United States, it was found that what we termed grade I fish was considered by them to have a degree of perfection rarely found in the commercial article; and that their grade I fish is comparable to our grade II. Furthermore, they accepted as merchantable fish whose quality extended far into our grade III. A similar situation was observed in the British fishing industry. On the other hand, some of the Scandinavian countries, notably Denmark, condemn fish of some species which even the most reputable Canadian firms still consider merchantable. Even within our own industry there are variations in what is meant by the terms used to identify degrees of freshness. The concept of quality held by the plant foremen who assisted in this work represents the highest that can be found in our industry at the present time.

The relation between assigned quality and TMA values found in these tests takes on added significance if we examine in the accompanying Figure the characteristic TMA curve for iced cod or haddock. For approximately 5 to 7 days there is a slow consistent increase in the TMA values (A–B). This is followed by an accelerated increase for 3 to 5 days (B–C) and then another, almost linear, increase during which TMA is formed very rapidly (C–D).



Mean TMA values for large haddock and market cod, stored from 3 to 9 days in the hold at the time of discharge from the trawlers. This is a typical curve for gutted fish and is based on results from more than 7,000 determinations.

Approximately 90% of the fish graded I by the foremen and experienced fishery officers lie along the line A–B, with the remainder on the portion of B–C adjacent to B. Approximately 90% of the fish graded III lie along the line C–D with the remainder in B–C. Approximately 75% of the grade II fish lie along the line B–C with the remainder on the adjacent portions of A–B and C–D.

In other words, the point where these foremen and experienced fishery officers judged that the fillets cut from the fish would first show visible signs of deterioration is approximately where the TMA formation shows the first sharp increase. Once the TMA formation had reached the second almost linear stage, these men considered the majority of the fish to be no longer fit for processing for fresh or frozen fillets.

It is not presumed that the TMA values separating the grades are established by this work. Nor has it been shown that there should be only three grades. Both these points need further consideration in the light of economic practice and experience from extensive commercial grading. The work does show, however,

that experienced graders can consistently separate fish into three different grades and that the TMA values of the fish muscle have a very significant correlation with the assigned grade.

It has also been shown that less experienced Fisheries Department personnel do not obtain the same degree of accuracy in separating the fish into these grades. This will be considered more fully in a subsequent paper dealing with the grading efficiency and training of individual graders.

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Grading Fish for Quality. 2. Statistical Analysis of the Results of Experiments Regarding Grades and Trimethylamine values[1]

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ABSTRACT

The results of recent work at this station regarding the organoleptic grade of cod and haddock and the trimethylamine content of these fish were subjected to statistical treatment. It was established that there is a relation between grade and trimethylamine content which may be represented by a linear regression equation, if the trimethylamine content is expressed as log (1 + TMA value). The confidence with which this TMA index may be used to estimate grade was also determined. Based on these findings, a scale of TMA values for use in practical grading was set up; the suggested values are grade I: TMA value 0.00 to 1.00; grade II: TMA value 1.01 to 7.00 and grade III: TMA value 7.01 and higher. Finally, a method is suggested by means of which the ability of a grader to judge the quality of fish may be assessed.

In the preceding paper of this series Castell *et al.* (1958, in this issue) described tests in which a large number of cod and haddock were graded for quality by panels of graders and in which trimethylamine (TMA) values of the fillets cut from these fish were determined.

From the results, several conclusions were drawn:

1. TMA values may be used as an objective measure of quality.

2. TMA values between 0 and 1 indicate fish of prime quality; TMA values between 1 and 5 indicate fish that are spoiling but still capable of producing merchantable fillets; TMA values exceeding 5 indicate fish unfit for processing as fresh or frozen fillets.

3. Experienced graders can consistently separate fish into three different grades.

4. Less experienced graders do not obtain the same degree of accuracy.

Each of these conclusions, although true in general terms, would take on added importance if its limits of validity could be defined and if probabilities of occurrence or non-occurrence of events could be described.

To determine these limits, Castell's data have been subjected to a thorough statistical analysis the results of which are described here.

DEFINITIONS

Fish: Cod (*Gadus callarias*) and haddock (*Melanogrammus aeglefinus*).

TMA value: The trimethylamine content of a fillet, determined by Dyer's colorimetric method (Dyer, 1945) adapted to routine use (Hoogland, 1956), and expressed as milligrams of trimethylamine nitrogen per 100 grams of fillet.

TMA index: $\text{Log}_{10}(1 + \text{TMA value})$.

[1] Received for publication February 26, 1958.

J. Fish. Res. Bd. Canada, 15(4), pp. 717–728, 1958.
Printed in Canada.

Grade I, II and III: The quality of a fish, determined organoleptically by a grader, and expressed by the grade number. For a description, see Castell *et al.* (1958).

RELATION BETWEEN GRADE AND TMA VALUE

In the first experiment, a panel of 8 well-experienced commercial fish plant foremen judged the quality of 150 dressed cod and haddock. Each grader gave each fish the grade number I, II, or III, and hence for each fish, the record shows 8 grade numbers. For the 150 fish used in this experiment, the complete grading record is given in table I of the Castell *et al.* paper, together with the "assigned grades", i.e. the grades obtained by combining the scores into groups with majority decision of the panel (assigned grades I, II, and III) and those where the panel members showed differences of opinion (assigned grades "I or II" and "II or III"). Obviously, the quality of fish within one assigned grade is not constant; e.g. a fish receiving a grading record ("vote") 8-0-0 is of a better quality than one receiving a vote 6-2-0, and a vote 0-6-2 indicates a fish of poorer quality than a vote 2-6-0. To make full use of this information, the grading vote for each fish was converted into a numerical value, calculated from the record as follows. If the vote was *a-b-c*, in which *a*, *b*, and *c* are the numbers of votes from the panel of 8 foremen for grades I, II, and III, respectively, the numerical value (x) is calculated from

$$x = \frac{a + 2b + 3c}{8}$$

and used to indicate the "numerical grade" of the fish. Values obtained in this manner for the different possible grading votes are given in Table I.

It may be seen that the numerical grade climbs in steps of 0.125 and that in many cases there are two possible ways of arriving at the same numerical score. It should also be noted that the list does not include all possible combinations of votes for grades I, II, and III, of which the sum is 8. All combinations with zero in the centre (except for grades 1.000 and 3.000) have been omitted, as well as those where more than 1 vote would have been given to grade I if the

TABLE I. Numerical grades calculated from grading records of 8-member panel.

Grading record I II III	Numerical grade	Grading record I II III	Numerical grade
8 - 0 - 0	1.000	0 - 7 - 1	2.125
7 - 1 - 0	1.125	1 - 5 - 2	2.125
6 - 2 - 0	1.250	1 - 4 - 3	2.250
6 - 1 - 1	1.375	0 - 6 - 2	2.250
5 - 3 - 0	1.375	1 - 3 - 4	2.375
5 - 2 - 1	1.500	0 - 5 - 3	2.375
4 - 4 - 0	1.500	1 - 2 - 5	2.500
4 - 3 - 1	1.625	0 - 4 - 4	2.500
3 - 5 - 0	1.625	1 - 1 - 6	2.625
3 - 4 - 1	1.750	0 - 3 - 5	2.625
2 - 6 - 0	1.750	0 - 2 - 6	2.750
2 - 5 - 1	1.875	0 - 1 - 7	2.875
1 - 7 - 0	1.875	0 - 0 - 8	3.000
1 - 6 - 1	2.000		
0 - 8 - 0	2.000		

majority voted grade III and those where more than 1 vote would have been given to grade III, if the majority voted grade I. This was possible because such combinations were not encountered during a period of several months in tests with many hundreds of fish.

The data of Castell's table I were rearranged on the basis of these numerical grades; they are listed in Table II of the present paper.

TABLE II. Grades and TMA values of 150 fillets cut from 150 cod and haddock that had been graded by a panel of eight experienced plant foremen.

Per numerical grade			Per assigned grade			
Numerical grade	No. of fish	Mean TMA value	Assigned grade	Mean num. grade	No. of fish	Mean TMA value
1.000	63	0.39				
1.125	14	0.74	I	1.042	84	0.469
1.250	7	0.64				
1.375	1	0.22				
1.500	3	1.00	I or II	1.500	5	0.828
1.625	1	0.92				
1.750	5	3.17				
1.875	5	2.28				
2.000	9	3.29	II	1.986	26	3.335
2.125	2	6.50				
2.250	5	3.36				
2.375	2	1.84				
2.500	4	8.30	II or III	2.534	11	7.098
2.625	5	8.24				
2.750	8	9.44				
2.875	5	11.02	III	2.891	24	12.04
3.000	11	14.40				

To indicate the relation between grade and TMA value, these data have been plotted in Fig. 1. From the curve it was concluded that, with certain variations, the TMA value of a fish increased when the quality of the fish decreased (the numerical value of grade increased). The shape of the curve indicated that there might be a fairly simple algebraic expression describing this relation and was suggestive of the function $y = ab^x$. If this function really represented the relation, then conversion into $\log y = x \log b + \log a$ would be very useful, where the latter is linear and would enable the use of statistics of the straight line. To test this possibility, the TMA value of each fish was converted into the TMA index (which is defined as log (1 + TMA value), unity having been added to each TMA value to avoid negative values of the logarithm), and the means of these indices were plotted against the numerical grades. The result, given in Fig. 2, was very encouraging; the average relation between TMA index and grade appeared to be linear.

To test the validity of this conclusion, correlation tables were constructed from the original data[2]; Table III presents such a correlation for the panel of 8 foremen (the TMA indices have been grouped into classes with the range 0.100).

[2] Original data indicates that the grade and TMA value of each individual fish were used, and not the means for certain grades. These figures are not given in Castell's (1958) paper but they were kindly supplied by him for the present analysis.

TABLE III. Correlation table from data of panel of eight foremen.

TMA index			Grade = x									Coded = X								
Class	Midvalue = y	Coded = Y	1.000	1.125	1.250	1.375	1.500	1.625	1.750	1.875	2.000	2.125	2.250	2.375	2.500	2.625	2.750	2.87	3.000	f_y
			−8	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5	6	7	8	
0.000–0.100	0.050	−6	30	5	1	1														37
0.100–0.200	0.150	−5	19	2	4		2													27
0.200–0.300	0.250	−4	8	3				1		1	1									14
0.300–0.400	0.350	−3	5	2	1				1	1	2		2	1			1			16
0.400–0.500	0.450	−2		1	1				2	1	2	1								8
0.500–0.600	0.550	−1	1	1			1				1		1	1			1			7
0.600–0.700	0.650	0								1	1				1					3
0.700–0.800	0.750	1							1	1	1		1			1				5
0.800–0.900	0.850	2							1						1	1				3
0.900–1.000	0.950	3											1		1	1	2	2	1	8
1.000–1.100	1.050	4										1				1	1	1	1	5
1.100–1.200	1.150	5									1				1	1	1	1	3	8
1.200–1.300	1.250	6															2	1	6	9
		f_x	63	14	7	1	3	1	5	5	9	2	5	2	4	5	8	5	11	150

The original data for the second and third grading panels used in Castell's (1958) tests were treated in a similar manner and from each of the three correlation tables a number of statistics was calculated; the results are listed in Table IV.

TABLE IV. Statistics calculated from the data of three grading panels.

Statistic	Eight foremen	Eight fishery officers	Four fish inspectors
n	150	200	250
$\bar{x}$	1.626	1.903	2.010
$\bar{y}$	0.427	0.498	0.616
r	0.898	0.780	0.909
$t_r = \frac{r}{\sqrt{1-r^2}} \times \sqrt{n-2}$	24.8	17.5	34.3
z (uncorrected)	1.462	1.166	1.522
z (corrected for bias)	1.459	1.164	1.520
Regression of y on x	$y = 0.484x - 0.360$	$y = 0.452x - 0.363$	$y = 0.494x - 0.378$
Regression of x on y	$x = 1.668y + 0.914$	$x = 1.348y + 1.233$	$x = 1.673y + 0.980$
S.E. of estimate of x	0.325	0.351	0.309

The values of r, the correlation coefficient, were very highly significant for all three panels and indicated the existence of a strong association between grade (x) and TMA index (y). To test whether a straight line was the correct representation of this relation, analysis of variance was carried out on each of the three sets of data. The results, given in Table V, indicate that the regression was really linear for the panel of 8 foremen but that for the other two panels the deviations from linear regression were statistically significant. However, the linear regression accounted also in the latter cases for the major portion of the variation and the small deviation from linearity was not considered of practical importance.

If the judgement of the panel of 8 foremen is accepted as being correct (in other words, if this panel indicated the true grade of a fish) it may now be concluded that the relation between the true numerical grade of a fish and the TMA index of its fillets may be expressed by the regression equation (y on x)

$$\text{TMA index} = 0.48 \times \text{num. grade} - 0.36$$

and also that the true grade of a fish may be estimated from the TMA index of its fillets with the regression equation of x on y

$$\text{Grade} = 1.67 \times \text{TMA index} + 0.91.$$

This regression, of course, gives only a "best estimate" of the numerical grade; the degree of uncertainty of this estimate is given by its standard error (0.325, see Table IV). In 90% of all cases, the actual numerical grade will be within limits found by adding $\pm$ 1.64 $\times$ standard error to the value of the

TABLE V. Results of analyses of variance of the data of three grading panels.*

Grading panel	Variance	DF	Sum of squares	Mean square A	Source of variance between arrays	DF	Sum of squares	Mean square B	$z = \frac{1}{2}(\log_e A - \log_e B)$	Values of z for P = 5%	P = 1%
Eight foremen	Between arrays	16	1970.2	–	Lin. regr.	1	1901.5	–			
	Within arrays	133	388.6	2.922	Deviations	15	68.7	4.58	0.224	0.272	0.367
	Total	149	2358.8	–	Total	16	1970.2	–			
Eight fishery officers	Between arrays	16	1575.8	–	Lin. regr.	1	1286.3	–			
	Within arrays	183	536.1	2.930	Deviations	15	289.5	19.30	0.943	~0.3	~0.4
	Total	199	2111.9	–	Total	16	1575.8	–			
Four fish inspectors	Between arrays	8	3468.9	–	Lin. regr.	1	3346.5	–			
	Within arrays	241	581.2	2.412	Deviations	7	122.4	17.49	0.991	~0.4	~0.5
	Total	249	4050.1	–	Total	8	3468.9				

*For method of calculation, see Fisher (1954).

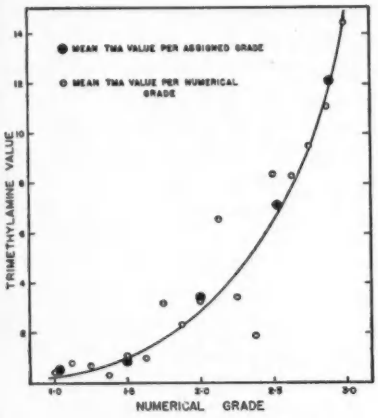

FIG. 1. Relation between TMA value and numerical grade (panel of 8 foremen).

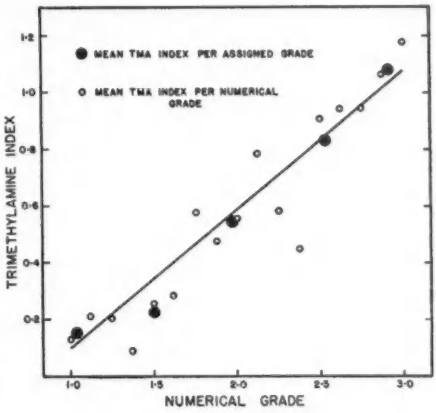

FIG. 2. Relation between TMA index and numerical grade (panel of 8 foremen).

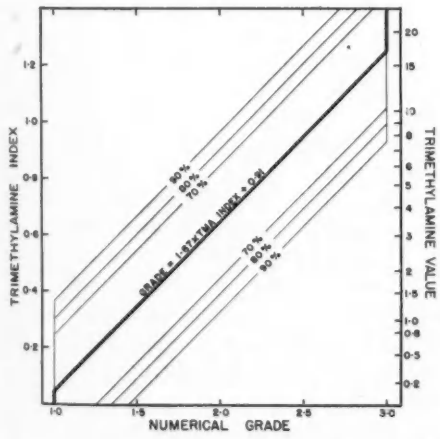

FIG. 3. Regression line for the determination of grade from TMA index with its 70, 80 and 90% confidence limits.

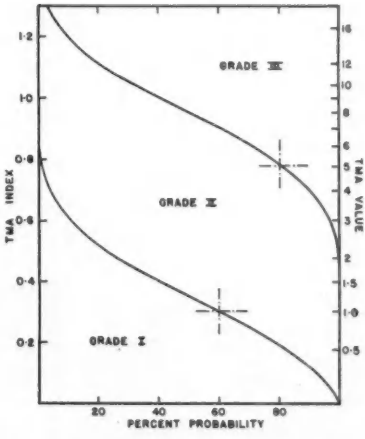

FIG. 4. Probabilities for the true grade of a fish to be I, II, or III as a function of the TMA index of its fillets.

estimate given by the regression equation. The regression line of x on y, together with these 90% confidence limits, as well as the limits for 70% and 80% of all cases, are given in Fig. 3. It may be seen that the numerical grade of a fish may be calculated from the TMA index to within about ± 0.5 unit in 90% of all cases. (The precision with which the average grade of a lot of fish may be estimated from the TMA indices of the individual fish in the lot improves with the square root of the number of fish.) It was also determined with which probabilities the TMA index (and hence the corresponding TMA value) indicated the true grade of a fish to be I, II, or III, at different levels of the index (accepting as the limits for these three grades the numerical values 1.00 to 1.50, 1.50 to 2.50, and 2.50 to 3.00). This was carried out as follows. For a given level of the TMA index, the estimate of grade was calculated and the numerical differences between it and the numerical values 1.500 and 2.500 (borderlines between grades I and II, and II and III, respectively) were expressed as multiples of the standard error of estimate (0.325, see Table IV). With the help of a table of the normal distribution, it was then established with what probabilities these values would be exceeded. This process was repeated for a series of different values of the TMA index and the results are given in the form of a diagram in Fig. 4. It should be emphasized that this diagram only gives the probabilities for one single fish of known TMA index being graded I, II, or III, and that it does not indicate the frequencies with which the various grades would occur in a batch of a large number of fish. In the diagram, it may be seen, for example, that a fillet with TMA value 3.0 indicated the grade of the fish from which it was cut, with approximate probabilities of 10% for grade I, 86% for grade II, and 4% for grade III.

During the past year or so the TMA values 1.0 and 5.0 have been used by Castell and others in this laboratory to indicate the upper limits of grades I and II; these points have been marked in Fig. 4. It may be seen that the probability for a fish with TMA value 5.0 (which on this basis was graded II) to have been really grade II is 80%; there is a 1% chance that it was a grade I fish and 19% chance that the true grade was III. Similarly, a fish with TMA value 1.0 has a 60% chance of actually having been grade I and 40% chance of having been grade II. Apparently, practical application of TMA values as the indicators of grade has not required the same degree of rigidness to distinguish between grades I and II as it did to distinguish between grades II and III. It seemed more logical to apply the same measure in both cases. At present, no specific criterion for making a choice is available. In practical use, the upper level of 1.00 for grade I has been quite satisfactory. If it is accepted that the same probability ratios must be used at both levels, it may be concluded from Fig. 3 that the upper limit for grade II should be increased. (Probabilities 60% for grade II and 40% for grade III.) However, the present arbitrary maximum permissible TMA value levels for both grades I and II may require further adjustment in the light of economic practice and as further experience is gained from extensive commercial grading.

A MEASURE FOR THE ABILITY OF GRADERS TO JUDGE THE QUALITY OF FISH

So far, these analyses have been concerned with establishing the type of the relation between TMA values and the grades assigned to fish by panels of graders. The judgement of the panel of foremen has been accepted as giving the true grade and it may now be questioned to what extent other panels would reproduce this judgement and also to what degree one individual grader would approach this judgement. The latter was considered of particular importance, since in practice it will not be possible to have more than one inspector grading fish in a fish plant.

Already from the data in Table IV there was some indication that the correlation coefficient (r) might be used to indicate the confidence with which the results of grading may be treated: a high correlation coefficient was found for the panels of very experienced men (8 foremen and 4 fresh-fish inspectors), whereas this coefficient was lower for the panel of 8 fishery officers who had considerably less experience in grading of fresh fish. Castell (1958) reports in his table X the results of grading 200 cod and haddock by two panels (of two members each) of graders. The first was formed by one foreman who had been a member of the original foremen panel and whose judgement had agreed with that of the whole panel in more than 90% of all cases, and the best inspector from the group of four used in the original experiments. The second panel consisted of two fishery officers who had no experience with the judging of the quality of fresh fish. The original data[2] of this test were treated as follows. Each score was converted into its corresponding numerical value (for a panel of two, the only possible values are 1.0, 1.5, 2.0, 2.5, and 3.0; for one single grader, they are 1, 2, and 3) and correlation tables were set up to determine whether or not a significant association existed between numerical grade and TMA index for (a) the panel of experienced men, (b) the panel of men with less experience, and (c) each man individually. The results of these calculations are summarized in Table VI. It may be seen that very significant correlations were found in each instance but that the association between grade and TMA index was much stronger for the experienced graders than for the others. An analysis of the values of z showed that there was no significant difference (0.05 probability level) between the correlation coefficients for A + B and A alone and C + D and either C or D alone. (All other differences were highly significant.) Combining the experienced graders A and B into the panel A + B had improved the correlation to at least the level of that of the best of the two graders but combining the inexperienced men C and D into the panel C + D had not caused a demonstrable improvement over the level of the poorer of these two men.

These findings confirm Castell's conclusion that experienced graders are able to judge the grades more consistently than are inexperienced graders.

Comparison of the correlation coefficients of Table VI with those given in Table IV shows that in all cases the association between grade and TMA index was stronger for the larger panels than for the smaller ones or the individuals but that one of the graders (A) approached the values for the whole panels.

TABLE VI. Statistics calculated from the data of several graders who graded the same 200 cod and haddock; A and B experienced, C and D inexperienced graders.

Statistic	Graders A + B	Grader A	Grader B	Graders C + D	Grader C	Grader D
n	200	200	200	200	200	200
$\bar{x}$	1.89	1.87	1.92	1.74	1.79	1.68
$\bar{y}$	0.504	0.504	0.504	0.504	0.504	0.504
r	0.786	0.765	0.616	0.374	0.244	0.381
t_r	17.9	16.7	11.0	5.68	3.54	5.80
z	1.059	1.008	0.718	0.393	0.249	0.401
Regression of y on x	$y = 0.37x - 0.20$	$y = 0.35x - 0.14$	$y = 0.25x + 0.02$	$y = 0.20x + 0.15$	$y = 0.11x + 0.30$	$y = 0.18x + 0.19$

DISCUSSION

The analyses of the grading records of three panels of graders have shown that a direct relation exists between the TMA index (and hence the TMA value) of a fillet and the grade of the round fish from which this fillet was cut. For each of the panels a linear regression equation could be set up to describe the interdependence of these values. At equal TMA levels, the numerical values for grade obtained from these equations were equal to with 0.2 unit, except for very low values of TMA. This demonstrated that TMA indices of fillets may be used, with certain qualifications, as objective indicators of the true grade of the fish (true grade having been defined as the grade given to a fish by the "standard" panel of 8 foremen). The standard error with which the numerical grade may be estimated from the TMA index was found to be fairly large (0.325); it should be emphasized, however, that these tests were carried out with mixtures of fish containing a much larger variety of qualities than would be expected to occur in samples of the same size in actual practice. It is very likely that elimination of fish (e.g. "bilgy" fish, "ping-pong" haddock) known in advance (from experience) not to follow the TMA pattern would have caused a considerable drop in the standard error of estimate of grade. Moreover, treatment of cod and haddock separately, rather than combined, might have improved the precision with which TMA indicates grade. Unfortunately, the samples were too small to permit these refinements; these points are now under investigation.

Even with the standard error as found for these heterogeneous mixtures of fish, it was possible to work out probabilities for fish with certain TMA values to be graded I, II, or III, and with the help of these figures, a scale for practical grading could be developed. For the present, the limits of TMA value for each grade have been taken as: grade I, 0.00–1.00; grade II, 1.01–7.00; and grade III, 7.01 and higher. The choice of these levels has been subjective and this may mean that revision will be necessary in the future. A possibility which suggested itself (see Fig. 4) was to use a slightly more complex scale of "TMA grades", in which grade I is subdivided:

Grade Ia, 0.00 to 0.50 (probabilities at upper level 80–20 for grades I and II).

Grade Ib, 0.51 to 1.00 (probabilities at upper level 60–40 for grades I and II).

Grade II, 1.01 to 7.10 (probabilities at upper level 60–40 for grades II and III).

Until more information is available, and until it has been established whether this scale would be practicable, the original three-grade scale will be used, however.

In commercial practice, it will not be possible to grade fish objectively by using large numbers of TMA determinations; but subjective, organoleptic grading will be carried out, probably by one grader in each fish plant. It will hence be necessary to have a procedure by means of which it may be ascertained that (a) this grader has the correct judgement and (b) all graders in all the plants use, within limits, the same judgement.

It has been shown that the correlation coefficient indicating the strength of the association between TMA index and grade may be used as the indicator of a

grader's ability to grade fish. Comparison of these coefficients and the regression equations for different graders will show whether their standards are the same. It remains to be established what minimum value of the coefficient is required for a grader to be acceptable (a value which might be a useful guide until more data become available seems to be 0.5, determined on a sample of at least 150 fish of mixed quality).

Rather than the method of product-moment correlation, used throughout this paper to determine the strength of the association between TMA index and grade, a method of rank correlation could be used[3]. Each fish would be assigned the rank number 1, 2, or 3 according to its organoleptic grade and also according to its TMA value (using some accepted scale). The strength of the association between the two rankings may then be expressed by a coefficient of rank correlation (either Spearman's R or Kendall's τ). This procedure has been tried out with the data of Castell's (1958) table XI in which TMA values of fish selected to be typically grades I, II, or III have been listed and his table XII which gives TMA values and grades of samples taken from large boxes of fish. For both tables, the two correlation coefficients were very high, indicating that the grader was well able to handle the grading; however, the number of fish was much too small to permit any further treatment of these samples.

CONCLUSIONS

1. There is a relation between the organoleptic grade of fish and the TMA value of its fillets.

2. The numerical grade may be estimated from the TMA value with the equation

$$\text{Grade} = 1.67 \times \text{TMA index} + 0.91$$

in which TMA index is $\log(1 + \text{TMA value})$.

3. In 90% of all cases, the grade thus calculated will be within 0.5 unit of the true numerical grade.

4. A scale of TMA values has been developed which may be used to classify fish as being grade I, II, or III. The TMA values suggested are 0.00–1.00, 1.01–7.00, 7.01–higher. This scale may need to be revised in the future.

5. The ability of a grader to judge the quality of a fish may be assessed by determining the correlation coefficient of the association between grade and TMA index for this grader.

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[3] This was suggested to us by Mr. J. N. Lewis of the Economics Division of the Department of Fisheries, whom we want to thank for his helpful advice and criticism.

Grading Fish for Quality. 3. Grading of Recently Cut Fillets[1]

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ABSTRACT

Panels of experienced fish-plant foremen and government fresh-fish inspectors graded cod and haddock in the round or as gutted whole fish, and subsequently graded the same fish as fillets. The results show that in general the two sets of gradings were very similar, and that both showed a close correlation with the trimethylamine (TMA) value of the fish muscle. When the fish was relatively fresh (TMA value 0.1 to 1.5), there was a slight tendency for the panels to be more severe in grading the fillets than the corresponding whole fish. As spoilage progressed, this trend reversed.

The results suggest that during the earlier stages of spoilage it is easier for a grader to judge the quality of a fish by examining the changes occurring on the exterior of the whole or gutted fish than by examining the fillet cut from it. This is particularly so where the grader cannot give careful attention to the early spoilage odours developing in the fillet.

There are definite exceptions to the usual close correlation between the quality of cod or haddock fillets and their TMA values. Bilgy fish, ungutted fish, and certain types of very soft-textured fish may be of very poor quality and still have a relatively low TMA value. These exceptions are discussed in their relation to a system of grading for cod and haddock based on organoleptic examination and supported by TMA values as objective standards of quality.

In the preceding papers of this series (Castell *et al.*, 1958; Hoogland, 1958) it was shown that plant foremen and experienced fresh-fish graders were able to separate round and gutted cod and haddock into three grades of quality and that the corresponding trimethylamine (TMA) values of these grades were approximately 0 to 1, 1 to 7, and over 7.

The present paper is concerned with the organoleptic examination and grading of fillets cut from fish previously graded as gutted or round fish. It is obvious that, in any system of grading for quality, there ought to be a fairly close correlation between grades given to whole fish and the grades given to fillets recently cut from these fish.

This immediately brings up the problem of the relative ease with which fish may be graded for quality by examination of the whole fish or by examination of the fillets cut from them. During the earlier stages of spoilage of gutted fish, most of the bacterial action takes place on the outer surfaces, in the gills, and in the lining of the gut cavity (Stewart, 1932; Lücke and Frercks, 1940; Wood *et al.*, 1942; Dyer *et al.*, 1946). From these surfaces the soluble spoilage products diffuse inward to reduce the quality of the muscle beneath. Evidence of this "surface spoilage" can be easily seen in the change in the appearance of the eyes, gills, gut cavity, and outer surfaces of the fish. In comparison, there is relatively little visible change in the fillets if they are cut from the fish during the earlier stages of spoilage. Any changes that have taken place during this period of incipient spoilage are more easily detected by the presence of off-odours or by means of

[1] Received for publication February 26, 1958.

J. Fish. Res. Bd. Canada, 15(4), pp. 729–748, 1958.
Printed in Canada.

chemical tests. One would expect, therefore, that a commercial grader would more easily recognize and follow incipient spoilage of fish by examining the exterior of the whole fish than by examination of the excised fillets. This would be particularly so if the grader were unable to give careful attention to the off-odours that are present in the fillet.

It must be clearly understood that all the fillets dealt with in this paper were recently cut from the whole fish; any change that had taken place in the fillet had occurred before it was removed from the whole or gutted fish. A fillet that spoils after it has been cut from the fish is a different problem and will be considered later.

In addition to comparing the grades given to whole fish and fillets, this paper also deals with a second problem. In grading and testing fish it has been observed occasionally that one encounters fillets wherein the usual relation between quality and TMA values no longer holds. They are fillets of poor quality having relatively low TMA values. Specific examples of this type of spoilage have been investigated and some consideration has been given to the question of how they might disrupt a grading scheme in which TMA values are used to supplement the organoleptic grading.

EXPERIMENTAL METHODS

The definitions of the grades given to the whole fish, the use of panels for arriving at the grades, the significance of the term quality and the meaning and measurement of TMA value, are the same as those described in a preceding paper (Castell *et al.*, 1958, in this issue).

The grades given to the fillets were also based on the sensory judgements of the experienced plant foremen or experienced Department of Fisheries personnel. If they judged the fillets to be free from perceptible spoilage they were recorded as grade I. Where they judged them to be showing some signs of spoilage, but still merchantable, they were judged grade II. Those fillets considered unfit for processing for the fresh or frozen fish trade were recorded as grade III.

The procedure used in these tests was to lay out the whole fish on long tables in this Station's pilot plant, where they were examined by the plant foremen or fishery officers. An experienced cutter then removed the fillets and these were rearranged in such a manner that the graders were unable to associate any fillet with the particular fish from which it had been cut. Immediately after this, they were graded and the TMA values were determined.

EXPERIMENTAL RESULTS

In the first test, 100 gutted cod and haddock, varying in quality from very fresh to spoiled, were graded by a panel of six plant foremen. Immediately afterwards, they graded the fillets cut from these fish. Table I shows the grades given to each fish and the corresponding fillet and the TMA value of that fillet.

In 56% of the fish, there was complete agreement between the grades given to the whole fish and to the corresponding fillet. In another 29% there was only a very slight difference in the gradings. Examples of this may be seen in the first

TABLE I. The TMA values and grading results for 100 cod and haddock that were graded by a panel of 6 experienced plant foremen. They were graded* first as whole fish and then as the fillets cut from these fish.

No.	Round	Fillet	TMA	No.	Round	Fillet	TMA	No.	Round	Fillet	TMA
1	I	I	0.02	34	II	I	0.94	67	II	I or II	4.23
2	I	I	0.02	35	I	I	1.00	68	II or III	II	4.48
3	I	I	0.04	36	I	I	1.02	69	II	II	4.75
4	I	I	0.10	37	I	I or II	1.05	70	III	III	5.02
5	I	I	0.14	38	II or III	I or II	1.06	71	III	II	5.40
6	I	I	0.16	39	II	I	1.08	72	II	II	5.65
7	I	I or II	0.16	40	II	II	1.10	73	III	I	6.25
8	I or II	I	0.18	41	I	I	1.10	74	II	II or III	6.30
9	I	I	0.20	42	I or II	I or II	1.18	75	II	II	6.44
10	I	I	0.20	43	II	I or II	1.22	76	III	III	7.20
11	I or II	I or II	0.22	44	II	I	1.28	77	III	II	7.24
12	I	I	0.22	45	I or II	I	1.35	78	II or III	I or II	7.34
13	I	I	0.22	46	I	I or II	1.38	79	II or III	II or III	7.34
14	I	I	0.24	47	II	I	1.46	80	II or III	I or II	7.74
15	I	I or II	0.24	48	II	I or II	1.56	81	III	II or III	8.25
16	I	I	0.24	49	I	II	1.58	82	III	II	8.50
17	I	I	0.26	50	II	II	1.66	83	III	III	9.48
18	I	I	0.34	51	II	II	1.86	84	II or III	II or III	9.60
19	I	I	0.36	52	II	I or II	2.12	85	III	II or III	9.73
20	I	I or II	0.36	53	II	II	2.20	86	III	III	9.87
21	I	I or II	0.40	54	II or III	I or II	2.36	87	III	III	10.30
22	I	I	0.40	55	II or III	I or II	2.38	88	III	II or III	10.54
23	I	I	0.44	56	I	I or II	2.56	89	III	III	10.58
24	I	I or II	0.44	57	II	II	2.83	90	III	II or III	12.28
25	I	I	0.50	58	II or III	II or III	2.94	91	III	III	12.38
26	I	I	0.50	59	II or III	II	3.20	92	II or III	II or III	12.56
27	I	I or II	0.54	60	III	II	3.82	93	II or III	I or II	12.96
28	I	I or II	0.56	61	II	II	3.83	94	III	III	13.84
29	I	I	0.60	62	II	I or II	3.85	95	III	III	15.22
30	I	I or II	0.60	63	III	II or III	4.02	96	III	II	15.64
31	I	I	0.60	64	II	I or II	4.06	97	III	III	16.23
32	I	I	0.78	65	II	II	4.08	98	III	III	16.25
33	I	I	0.82	66	II	I or II	4.14	99	III	III	16.50
								100	III	III	17.14

*The grades recorded as I, II, or III indicate that five or six of the six men agreed on the given grade; "I or II" and "II or III" indicate that there was a split decision.

column of Table I, where the panel graded the whole fish as I and the fillet as "I or II" or vice versa. Other examples may be seen in the second and third columns, where the corresponding whole fish and fillets were graded respectively II and "I or II", or III and "II or III". (For the sake of convenience, examples such as these will be spoken of as differing by half a grade.) In 14% of the fish there was a difference of one grade. Only in the case of one fish (TMA 6.25) was there a complete reversal in grading, where the fillet cut from a grade III fish was judged to be of grade I quality.

Further comparison of the individual gradings indicates that when the fish were relatively fresh (TMA of approximately 1.0 or less), the graders were a little more severe in their judgment of the fillets than of the whole fish. As spoilage progressed beyond this point, the trend was reversed and they graded the whole fish more severely than the fillets cut from them.

Table II indicates that a relation exists between the grades given to both the whole fish and the fillets and the TMA values. For the whole fish the agreement

TABLE II. Frequency distribution of TMA values for 100 cod and haddock, graded first as whole fish, and then as fillets. The grading was done by a panel of 6 experienced plant foremen.

	TMA levels of the fish			Number of fish
	0 to 1	1.1 to 7	Over 7	
Grades given as whole fish	%	%	%	
I	82	18	0	38
I or II	50	50	0	4
II	5	95	0	22
II or III	0	50	50	12
III	0	21	79	24
Grades given as fillets				
I	76	24	0	34
I or II	34	54	12	26
II	0	88	12	17
II or III	0	30	70	10
III	0	8	92	13

between grades and TMA values is quite similar to that reported in previous similar trials (Castell *et al.*, 1958). The relation between the grades given to the fillets and their TMA values is also evident.

The second test was purposely made much more difficult so as to see what the results would be under extreme conditions. Sixty cod and haddock were carefully selected. These included relatively fresh fish that had been crushed and bruised, and others that had been left exposed to direct sunshine for several hours. They also included fish that had developed various degrees of bilgy odours, and small ungutted haddock ("ping-pongs"), less than 4 days in storage, but which had been improperly cared for in the trawler. Four fish of poor quality (No. 42, 47, 52, and 56 in Table III) were thoroughly washed on the exterior and in the gill area and gut cavity immediately before grading; three others (No. 55, 57, and 58 in the same Table) were washed only in the gut cavity.

In spite of the difficulties put in the way of the graders, the results, listed in Table III, were much the same as in the previous test. In 48% of the gradings there was complete agreement between the grades given to the whole fish and to the corresponding fillets; 38% differed by half a grade; 8% differed by one grade; and there were no reversals from grade III to grade I. Washing the fish had no effect on the grades given. Several of the foremen noted on their grading slips: "these fish have been washed".

In Table III, there are some obvious exceptions to the previously noted relation between the quality of the fish, as indicated by the grade, and the TMA values. These are the fish numbered 6, 20, 28, 30, 31, 33, and probably 40 and 45. The first five of these were small, ungutted haddock that had developed faecal odours in the muscle adjacent to the gut cavity and the last three were bilgy fish. These will be discussed in greater detail in the section dealing with various types of spoilage, where fish of decidedly poor quality have relatively low TMA values.

In the third set of gradings, a panel of 10 fresh-fish inspectors graded a mixed

TABLE III. The TMA values and grading results of 60 cod and haddock, graded first as whole fish, and later as fillets by a panel of 6 plant foremen.

No.	Round	Fillet	TMA	No.	Round	Fillet	TMA
1	I	I or II	0.46	31	III	III	2.05
2	I	I	0.50	32	I or II	I	2.10
3	I	I	0.56	33	III	III	2.13
4	I	I	0.63	34	II	II	2.20
5	I	II	0.63	35	II	I or II	2.35
6	III	II or III	0.75	36	I or II	I or II	2.48
7	I	I	0.75	37	I	I	2.50
8	I	I or II	0.78	38	I	I	2.62
9	II	I or II	0.80	39	II	II	2.62
10	I	I	0.85	40	III	II or III	2.65
11	I or II	I	0.88	41	II	I	2.83
12	I	I or II	0.94	42	II or III	II or III	3.00
13	I	I or II	1.02	43	II	I or II	3.48
14	I or II	I or II	1.05	44	II	II	3.58
15	I	I	1.10	45	II	III	3.68
16	I	I or II	1.13	46	II or III	II	3.73
17	I or II	II	1.23	47	III	III	4.02
18	I	I	1.38	48	II	I or II	4.23
19	II	II	1.45	49	III	II	4.48
20	III	II or III	1.50	50	II	II	4.75
21	I	I or II	1.50	51	III	III	5.16
22	II	II	1.53	52	II or III	III	5.17
23	II	I	1.58	53	III	I or II	6.25
24	II	I or II	1.63	54	III	III	7.32
25	II	I or II	1.73	55	III	III	9.48
26	II or III	I or II	1.76	56	III	III	9.73
27	II	I or II	1.83	57	III	III	9.87
28	III	II or III	1.85	58	III	III	10.30
29	II	I	1.88	59	III	III	13.60
30	III	II or III	1.95	60	III	III	14.60

lot of 35 cod and haddock. The relation between the grades given to the whole fish and to the fillets was as follows:

Complete agreement	66%
Difference of half a grade	23%
Difference of one grade	11%
Difference of two grades	None.

In 75% of the judgements where there was a difference in the grades given to the whole fish and to the fillets; the panel was more severe in grading the whole fish.

These three sets of gradings were very typical of others carried out under similar conditions with panels of plant foremen or experienced fishery officers. It may be seen that in these tests, 85, 86, and 89% of the grades given to the fillets were either the same or within half a grade of those given to the round fish. In only one instance was there a difference of two grades between the whole fish and the corresponding fillet.

A fourth set of gradings (Table IV) has been added to show the results obtained when one grader replaces the panel. (This particular man had been a plant foreman for many years and subsequently joined the staff of the Department of Fisheries. He has the top record for efficiency in grading fresh fish.) The

TABLE IV. Grading of gutted cod and haddock and their fillets carried out by an experienced fresh-fish inspector.

No.	Round	Fillet	TMA	No.	Round	Fillet	TMA
1	I	I	0.20	36	II	II	1.80
2	I	I	0.29	37	II	I	2.10
3	I	I	0.35	38	III	III	2.13
4	II	II	0.45	39	II	II	2.35
5	I	I	0.48	40	I	I	2.50
6	I	II	0.50	41	II	II	2.50
7	I	I	0.50	42	I	I	2.60
8	I	I	0.60	43	III	III	2.74
9	I	I	0.63	44	III	I	2.75
10	I	I	0.63	45	II	II	3.42
11	I	II	0.63	46	II	II	3.58
12	I	I	0.73	47	II	III	3.70
13	I	I	0.73	48	II	II	3.73
14	I	I	0.75	49	III	III	3.83
15	II	I	0.80	50	III	I	3.85
16	I	II	0.80	51	II	I	4.23
17	I	I	0.83	52	II	I	4.61
18	I	I	0.88	53	II	II	5.05
19	I	II	0.90	54	III	III	5.20
20	II	I	1.00	55	III	III	5.23
21	II	I	1.05	56	III	III	5.53
22	I	I	1.10	57	III	III	6.30
23	II	II	1.13	58	III	III	6.35
24	I	I	1.15	59	III	III	7.03
25	I	II	1.16	60	II	II	7.10
26	II	II	1.23	61	III	III	7.30
27	I	II	1.25	62	III	III	7.38
28	I	II	1.33	63	III	III	10.60
29	I	I	1.38	64	III	III	13.38
30	II	II	1.45	65	III	III	14.48
31	I	II	1.50	66	III	III	14.60
32	II	II	1.53	67	III	III	16.23
33	I	I	1.58	68	III	III	16.25
34	II	I	1.63	69	III	III	17.28
35	II	I	1.73	70	III	III	19.75

results show complete agreement in 73% of the grades given to whole fish and corresponding fillets. There was a difference of one grade in 24% and a difference of two grades in 3% of the gradings. This man showed the same tendency as noted previously in being more severe in grading the fillets when the fish were fresh and more severe with the whole fish when spoilage became more advanced:

TMA range	No. fillets scored lower than corresponding whole fish	No. whole fish scored lower than corresponding fillets
0 to 1.50 (30 fillets)	8	4
1.50 to 19.70 (40 fillets)	1	7

The single fillet having a TMA value above 1.50 which scored lower than the whole fish was down-graded because it had a slightly bilgy odour that had not been observed in the whole fish.

FILLET ODOURS AND TMA VALUES

It has been pointed out that commercial graders tend to use their sense of sight much more than their sense of smell in arriving at the grades of fish. There

are many obvious reasons for this. In general, man's sense of sight is more highly developed and is used more than his sense of smell; it tires less easily, and the identity of what he sees is more easily defined and recorded.

This becomes more pronounced under the conditions that normally exist where fish are being graded. The flesh, and more especially fish slime, are notorious for the off-odours they produce as they decompose. Unless scrupulous care is taken, floors, boxes, bins, cutting tables, and many other surfaces in the plant absorb fish slime, which is continuously being decomposed, giving the plant its characteristic "fishy" odours. Some of the substances responsible for the odours of decomposing slime are not easily removed by washing. Even with care, a grader handling fish soon finds that his hands have taken on an unpleasant fishy odour. The result of this is that unless the odour from a fillet is quite strong it may go unnoticed by graders working in the plant.

It was decided, therefore, that when an attempt was to be made to determine what relation existed between the TMA values and the odours of freshly excised fillets, the work should be done in the laboratory with personnel trained in identifying odours from fresh and spoiled fish.

During a period of two years, 500 freshly excised cod and haddock fillets, in groups of 6 to 30, were carefully examined for odours and determinations were made of their TMA content. As well as this, a record was kept of the history of the fish from the time of catching until the fish were filleted and examined. Quite arbitrarily, the fillet odours were classified into four degrees of intensity: (1) no discernible off-odours, (2) very slight off-odours, (3) mild odours, and (4) strong odours. They were also divided into those which were decidedly offensive (faecal, putrid, bilgy, etc.) and those which were unpleasant, but not so offensive (stale, sour, musty, turnipy, etc.).

It was observed that the odours classified as "very slight" could rarely be detected by persons inexperienced in smelling fish. The first two divisions (no off-odours, and very slight off-odours) correspond approximately to the grade I quality as judged by the plant foremen. The fillets classified as having "mild off-odours" correspond approximately to grade II fish, and those having "pronounced or offensive" odours approximate grade III.

Figure 1 shows graphs of the frequency distribution of various TMA levels for each of these groups of fillets. The following is the most pertinent information taken from these curves.

(a) The majority, 78.6%, of the fillets showing no perceptible off-odours had TMA values between 0.0 and 1.0; and 50.3% had TMA values under 0.5. Ninety-nine per cent had TMA values under 2.0.

(b) The majority, 82.5%, of the fillets with very slight off-odours had TMA values between 0.5 and 2.0. In contrast to the group without off-odours, only 3.5% of this group had values under 0.5.

(c) The majority, 85.7%, of the fillets with mild off-odours had TMA values between 1.0 and 7.0; 7.4% were below 1.0, and 6.7% were above 7.0. A few fish in this category were found with TMA values as high as 12.0.

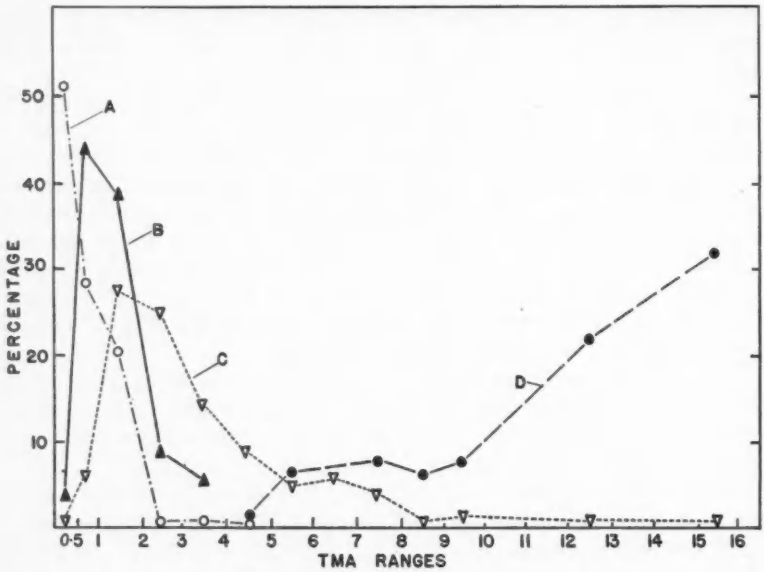

FIG. 1. Relation between TMA content and odour of freshly excised cod and haddock fillets. The four curves show the frequency distribution of 500 fillets in various TMA ranges (0 to 0.5, 0.5 to 1, 1 to 2, 2 to 3, 3 to 4, etc.) for each of the following odour classifications:

A—No spoilage odours (214 fillets)
B—Very slight off-odours (58 fillets)
C—Mild spoilage odours (161 fillets)
D—Strong spoilage odours (67 fillets)

(d) The majority, 77.5%, of the fillets with strong and offensive off-odours had TMA values above 7.0; 56% were above 10.0, and 19.5% were below 7.0.

Because of the previous observations on offensive-smelling fillets with relatively low TMA values, it is of some interest to note the data from the records of the 12% of strong-smelling fillets with TMA values under 7.0:

No.	Odour	TMA value	Notes
339	Faecal	4.3	Small, ungutted "feedy" haddock
476	Bilgy or faecal	0.9	
477	,,	1.1	
478	,,	1.0	These were all fish that had been stowed in the boat
488	,,	1.5	at the bottom of the pens and at the time of dis-
492	,,	2.2	charge were found resting against the boards
494	,,	2.0	
500	,,	2.2	

Seven other fish, with TMA values between 5.1 and 6.9, were included in this group. They all had the "normal" types of sour or sour-putrid spoilage odours. These were all from the centre of the pens and not in contact with any wooden surfaces.

This is further confirmation of previous observations that offensive-smelling fillets with relatively low TMA values usually come from either bilgy or ungutted fish.

Table V condenses the data for these fish into a form that is directly comparable with the frequency distribution of the TMA values used previously for the results of grading whole fish and fillets.

TABLE V. Condensation of the data of Table IV to make them comparable with similar data for grading of whole fish and fillets (Table II).

Intensity of off-odours	TMA levels of the fillets			Number of fish
	0 to 1	1.1 to 7	Over 7	
	%	%	%	
None and very slight	72	28	0	272
Mild	7	86	7	161
Pronounced	3	19	78	67

These results suggest that the careful use of the sense of smell in grading fillets may be more accurate than judgements based mainly on appearances. In Fig. 2, 3, and 4 are compared the results of grading fish as a whole gutted fish, as fillets graded by smell, and as fillets graded by appearance. This information was obtained from the following tests: 672 gutted cod and haddock were graded I, II, or III by a panel of plant foremen; 542 cod and haddock fillets were also divided into three grades by examination in the laboratory where particular attention was given to off-odours; a third group of 233 fillets was graded by plant foremen under conditions where most of the selection had to be based on appearance. These were three different lots of fish, and not a comparison of the same fish judged in these different ways. Figure 2 shows the distribution in different TMA levels for all those graded I from each of the three lots of fish. Figures 3 and 4 do the same for fish graded II and III respectively.

It may be seen that even though these data represent three entirely different lots of fish, graded by three different methods, the TMA distributions are remarkably similar. However, there are a few significant differences.

Of the whole fish graded I by the foremen, 92.3% fell into the TMA range 0 to 1. The corresponding value for their grading of the fillets was 63.3%, which is almost one third less. The fillets graded by odour fell midway between these, having 75.6% of the fish graded I in the range 0 to 1. It may also be seen that although most of the remaining fillets graded I by appearance fell within the 1 to 2, and 2 to 3 TMA ranges, a small percentage was also in the levels between 3 and 7. This demonstrates that, using TMA values as a measure of spoilage, the foremen were able to pick a much more uniform lot of grade I fish when they graded them as whole fish rather than as fillets.

The results with the grade II and grade III fish show very similar distributions for the three methods of grading. The information on the grade III fish suffers from having been obtained with an insufficient number of fillets.

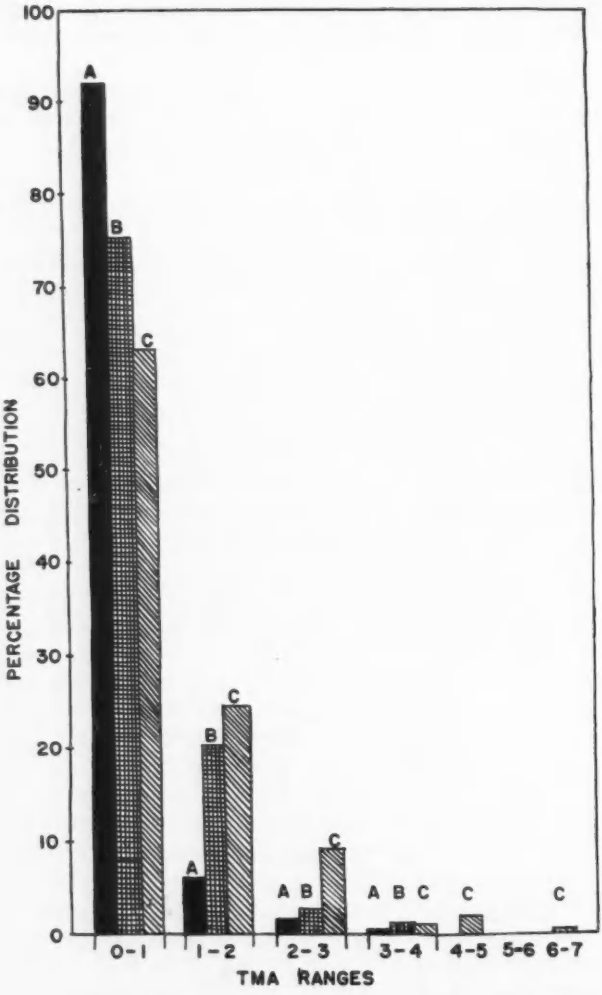

FIG. 2. The precentage distribution in various TMA ranges (0 to 1, 1 to 2, 2 to 3, etc.) of three different lots of cod and haddock that were all judged to be *grade* I quality. Each of the three lots of fish was judged differently. Those marked "A" consisted of 282 fish that were graded as whole or dressed fish by experienced plant foremen. Those marked "B" were 214 fillets, graded by trained workers in the laboratory by carefully examining the odours. Those marked "C" consisted of 92 fillets graded by plant foremen who rely more on visual observation than odour production as a basis for their judgements.

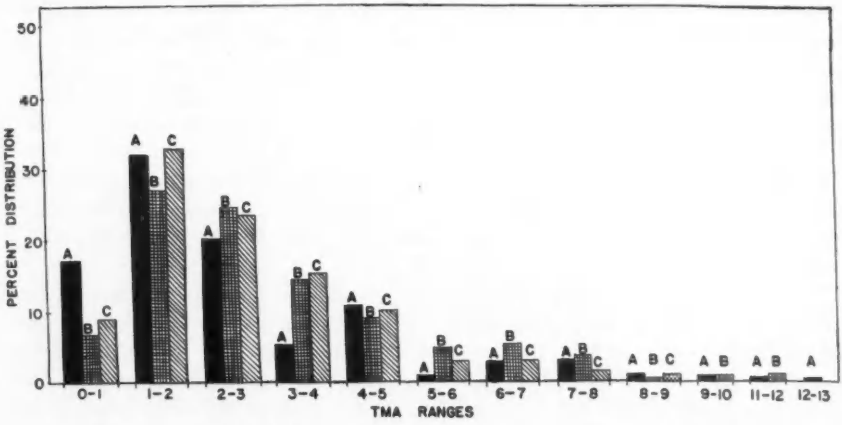

FIG. 3. The percentage distribution in various TMA ranges (0 to 1, 1 to 2, 2 to 3, etc.) of three different lots of cod and haddock that were all judged to be *grade* II quality. Each of the three lots of fish was judged differently. Those marked "A" consisted of 233 fish that were graded as whole or dressed fish by experienced plant foremen. Those marked "B" were 219 fillets, graded by trained workers in the laboratory by carefully examining the odours. Those marked "C" consisted of 116 fillets graded by plant foremen who rely more on visual observation than odour production as a basis for their judgements.

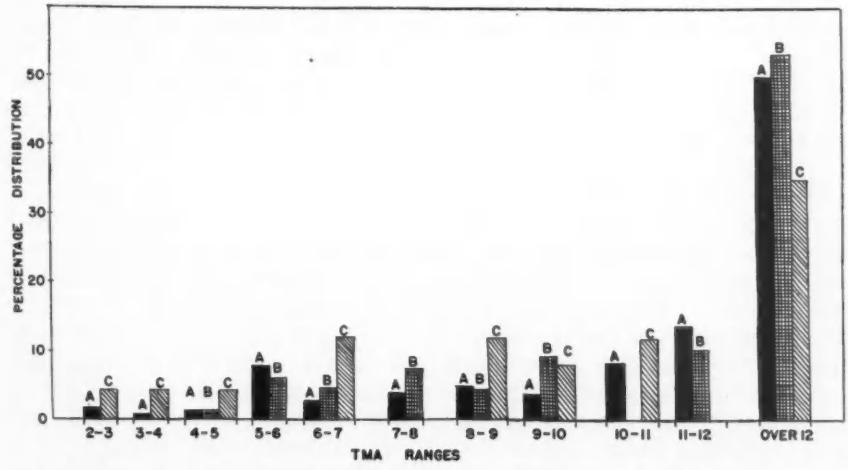

FIG. 4. The percentage distribution in various TMA ranges (0 to 1, 1 to 2, 2 to 3, etc.) of three different lots of cod and haddock that were all judged to be *grade* III quality. Each of the three lots of fish was judged differently. Those marked "A" consisted of 159 fish that were graded as whole or dressed fish by experienced plant foremen. Those marked "B" were 67 fillets, graded by trained workers in the laboratory by carefully examining the odours. Those marked "C" consisted of 25 fillets graded by plant foremen who rely more on visual observation than odour production as a basis for their judgements.

Grading of Fillets from "Bilgy" and Spoiling Ungutted Fish

One of the most important limitations to the use of TMA values as an objective measure of spoilage in cod and haddock fillets results from the occasional fish that may be encountered with very offensive off-odours, while having a relatively low TMA value. Up to the present time, almost all samples of fillets of this type encountered are from "bilgy" fish, that is, fish that have developed bilge-like odours after having been stored directly against the wooden pen boards in trawlers or in wooden storage pens in the plants. A somewhat similar type of fillet spoilage has been encountered where fish have spoiled under two other conditions.

Occasionally the cutters, who gut the fish aboard the trawlers, do not completely remove the portion of the intestine adjacent to the vent. If the fish have been feeding, this portion of the intestine (known to the fishermen as the "assgut") may contain considerable faecal matter. It has been observed that such fish, particularly if they have been pressed tightly in amongst other fish near the bottom of the pens, will develop an offensive faecal odour in the gut cavity, somewhat similar to the so-called "bilgy" odour. After 5 to 8 days stowage in the vessel, fillets cut from these fish show slight softening or discoloration and an offensive off-odour in the "poke area", that is, adjacent to the back portion of the gut cavity.

A somewhat similar condition sometimes occurs when fish have been stowed in ice without being gutted. This has been found particularly true of small feeding haddock of the type that has recently been used mainly for the manufacture of fish blocks. It has also been observed with cod and with large haddock, where ungutted fish have been allowed to spoil. At times it has been difficult to distinguish fillets cut from these fish from fillets cut from bilgy fish. It has been noted, however, that the offensive odour on the bilgy fish develops first and is most intense on the side of the fillet next to the skin, whereas fillets cut from spoiling ungutted fish develop the offensive odours on the inner side of the fillet adjacent to the gut cavity.

"Bilgy" fish. During a regular fishing trip to the Grand Banks in June, 60 gutted haddock were purposely stowed directly against the pen boards. At the time when the fish were being taken from the boat, 7 days later, 60 similar fish were picked from the centre of the pens, to be used as controls.

Immediately after landing, each fish in both groups of 60 was graded by a panel of five fresh-fish inspectors. The fillets were then cut from the fish, examined for odours and tested for TMA. In the case of the fish stowed against the pen boards, the fillet tested was from the side of the fish that had been adjacent to the wood.

Table VI gives the results for the fish from the centre of the pens. Taken as a whole, these were a typical lot of grade II fish with a few grade I fish interspersed among them. The relation between grade and TMA value is quite obvious. The odours from the fillets were either very slight or mild sour types. Table VII gives the corresponding results for the fish that had been stowed

TABLE VI. Grading record and TMA values of gutted cod and haddock selected from fish not touching the pen boards, judged by a panel of 5 fresh-fish inspectors.

No.	Whole fish grade	TMA value	Fillet odour	No.	Whole fish grade	TMA value	Fillet odour
1	I	0.42	None*	31	I or II	2.17	Mild
2	I	0.52	,,	32	II	2.17	,,
3	I	0.60	,,	33	I	2.25	,,
4	I	0.64	,,	34	II	2.50	V.S.
5	I	0.70	V.S.**	35	II	2.53	Mild
6	I	0.76	None	36	II	2.53	,,
7	I	0.80	V.S.	37	II	2.55	,,
8	I	0.82	None	38	II	2.62	,,
9	I	0.90	V.S.	39	I	2.63	,,
10	I	1.04	V.S.	40	II	2.63	,,
11	I	1.04	V.S.	41	II	2.67	,,
12	I	1.12	None	42	II	2.70	,,
13	II	1.40	V.S.	43	II	2.97	,,
14	II	1.42	None	44	II	3.00	,,
15	II	1.52	V.S.	45	II	3.03	,,
16	I	1.54	V.S.	46	II	3.05	,,
17	II	1.55	V.S.	47	II	3.17	,,
18	I	1.62	V.S.	48	II	3.37	,,
19	I	1.66	V.S.	49	II	3.40	,,
20	I or II	1.70	V.S.	50	II	3.52	,,
21	II	1.75	Mild***	51	II	3.68	,,
22	I	1.78	V.S.	52	II	3.75	,,
23	I	1.80	None	53	II	3.87	,,
24	II	1.80	V.S.	54	II	3.95	,,
25	I	1.86	V.S.	55	II	4.12	,,
26	II	1.92	Mild	56	II	4.15	,,
27	I	1.94	V.S.	57	II	4.22	,,
28	II	1.95	V.S.	58	II	4.30	,,
29	II	1.95	Mild	59	II	4.37	,,
30	I or II	2.07	V.S.	60	II	4.37	,,

*None—No perceptible off-odours.
**V.S.—Very slight off-odours.
***Mild—Recognizable spoilage odours which are neither very strong nor very offensive.

against the boards. Taken as a group, the inspectors condemned this lot as grade III, because of the presence of the bilgy odours.

There are several points of interest in the results obtained with the fish against the pen boards. First, it may be seen that 31 fish with TMA values between 1.0 and 5.50 have been graded III. Second, very few fish have been graded II. They are either I or III. This is the result of a natural human error in grading. The contrast between the very offensive bilgy fish and the non-bilgy fish creates a tendency to up-grade the better fish. Another point of interest is the result of a characteristic of the bilgy fish themselves. The bilgy odours are produced by either extremely volatile or very easily oxidized compounds. During the earlier stages of its development, before the odours have become very intense, a short exposure to air frequently eliminates the odour. When this occurs with whole fish, it has been observed that by ripping off the skin, the bilgy odours can be smelled on the muscle beneath. Later the odour may disappear from the surface of the fillet but still be present in the interior. It may be seen (Table VII) that bilgy odours were observed in 18 of the fillets cut from fish that were not noted as bilgy by the inspectors.

TABLE VII. Grading record and TMA values of cod and haddock that had been stowed against the pen boards, judged by a panel of 5 fresh-fish inspectors.

No.	Whole fish grade	TMA value	Fillet odour	No.	Whole fish grade	TMA value	Fillet odour
1	I	0.50	Bilgy	31	I	2.10	Mild
2	I	0.54	None	32	III (B)	2.10	Bilgy
3	I	0.66	,,	33	I	2.10	Mild
4	I	0.70	,,	34	I	2.20	Bilgy
5	I	0.70	Bilgy	35	III (B)	2.22	,,
6	I	0.82	None	36	I	2.26	,,
7	I	0.90	,,	37	I	2.30	,,
8	I	0.90	,,	38	III (B)	2.40	,,
9	III (B)**	1.00	Bilgy	39	III (B)	2.52	,,
10	I	1.16	None	40	I or II	2.54	,,
11	III (B)	1.20	Mild	41	III (B)	2.56	,,
12	I	1.20	V.S.*	42	III (B)	2.56	,,
13	I	1.20	Bilgy	43	III (B)	2.56	,,
14	I	1.24	V.S. bilgy	44	I	2.60	,,
15	III (B)	1.30	Bilgy	45	III (B)	2.66	,,
16	III (B)	1.32	,,	46	I	2.70	Mild
17	I	1.34	,,	47	III (B)	2.80	Bilgy
18	I	1.36	,,	48	III (B)	2.80	,,
19	III (B)	1.40	,,	49	III (B)	2.98	,,
20	III (B)	1.40	,,	50	III (B)	3.00	,,
21	I	1.60	,,	51	III (B)	3.00	,,
22	III (B)	1.60	,,	52	III (B)	3.02	,,
23	I	1.76	,,	53	III (B)	3.30	,,
24	I	1.84	,,	54	III (B)	3.56	,,
25	III (B)	1.90	,,	55	III (B)	3.70	,,
26	III (B)	1.90	,,	56	III (B)	3.76	,,
27	I	1.96	,,	57	III (B)	4.10	Sour
28	I	1.98	,,	58	III (B)	4.18	Bilgy
29	I	2.00	,,	59	III (B)	4.50	,,
30	I	2.04	,,	60	III (B)	5.50	,,

*V.S.—Indicates very slight off-odours.
**III (B)—Indicates that the fish has been graded III because of the presence of offensive bilgy odours.

IMPROPERLY GUTTED FISH. It has occasionally been observed that when the intestine has not been completely removed from gutted cod and haddock, a type of spoilage results that produces a particularly offensive odour and a relatively low TMA value. This has been observed only when the unexcised portion of the intestine contains faecal matter. After 5 or 6 days stowage in ice, such fish develop very offensive odours in the gut cavity particularly in the anal region.

In February, when fish were feeding heavily, gutted 7- and 8-day-old (post-mortem) cod and haddock with this defect were purposely picked out for examination and grading. It was observed that when the graders took care to examine the gut cavity, these fish were classed as grade III. When less care was taken, and the grading was based mainly on the appearance of the eyes, gills, and exterior surfaces, these fish occasionally passed as grade I or more often as grade II.

In one typical test, 20 improperly gutted 8-day-old haddock were taken from the vessel. Twenty other fish, similar except that they had had their intestines completely removed, were taken as controls. Fillets from these fish were

examined and their TMA values determined. The following are the grader's comments recorded at the time of examination:

> *Control fish*: "None of these fillets are from strictly fresh fish. Some are almost free from off-odours, but the majority have seaweedy, stale, or slightly sour odours. As a group, they are definitely grade II fillets."
>
> *Improperly gutted fish*: "These fillets smell putrid, similar to fish faeces that have been left exposed in the room for several hours. The flesh is visibly spoiled on the belly side in the anal area. This area is soft, discoloured and foul-smelling. They are definitely grade III fillets although some of the better ones might be salvaged by severely trimming the spoiled areas."

The TMA values for the control fillets ranged from 0.75 to 2.44, and averaged 1.25. The defective group ranged from 0.95 to 2.51 and averaged 1.64. There was obviously no close correlation between TMA values and the quality of the fillets cut from the fish containing a remnant of the intestine. Other similar tests carried out at this time brought similar results: faecal-smelling fillets were encountered with relatively low TMA values. It should be pointed out that mere presence of a small portion of the intestine in the gut cavity does not necessarily mean the fillets cut from the fish will be of poor quality. Three other factors are essential to this type of spoilage: faeces, time, and temperature. During the period of the year when the fish are not feeding, the intestines are empty and this type of spoilage does not occur. Even when the fish are feeding, and when faeces are present, rapid cooling and proper icing will delay the spoilage by several days (Castell *et al.*, 1956). However, when a gutted fish is removed from stowage and is found to retain a portion of the intestine, and when the anal end of the gut cavity has an offensive faecal odour, it may be taken for granted that the anal area of the fillet will be of very poor quality.

FILLETS FROM UNGUTTED FISH. Somewhat related to the spoilage discussed in the preceding section is the type that occurs when ungutted fish are stowed in ice. This is complicated by the presence of the fish's own digestive enzymes which in themselves will soften and discolour the portion of the flesh adjacent to the gut cavity. There is a great deal yet to be learned about this type of spoilage, the effect of feeding habits, the physiological state of the fish, the speed with which the fish are chilled after being caught, and the temperature at which they are stored. There are many contradictions in the present ideas of fishermen and producers on the effect of not gutting on the type of spoilage, and on the keeping-time of fish. Some of the scientific studies on this subject (including our own) are too restricted in the range of season, condition of the fish, and methods of handling, to give a very comprehensive picture.

Most of the trawler-caught cod and haddock landed in Nova Scotia are gutted shortly after being caught. The one exception, during the period covered by these tests, is the small ungutted haddock that have been used mainly for producing frozen blocks for the fish-stick trade. The majority of these fish, *if well taken care of in the boats*, usually produce good fillets, quite comparable to the gutted haddock, up to 5 or 6 days in storage, with TMA values similar to those of

gutted fish of the same grade. Beyond this storage period, the fillets from the ungutted haddock become softer and very frequently develop a strong faecal odour.

Unfortunately, these small "ping-pong" ungutted haddock are not always well taken care of on the boats. Frequently they are not rapidly chilled and not properly iced, resulting in spoilage of the gut and its contents, followed by softening and development of faecal odours in the fillets. Examples of this have been given previously in Table III. Forty more of these ungutted haddock that had not been properly iced were judged both in the round and as fillets, and their TMA values were determined. The results were the same as before: 8 fish were graded III and had TMA values ranging between 0.48 and 2.37, with an average of 1.40. The fillets cut from these fish were soft and faecal-smelling. Twelve fish graded either II or "II or III" had TMA values varying from 0.05 to 1.1 with an average of 0.54. The fillets from these fish had odours that varied from slightly to strongly faecal. The remaining fish of that group were also strongly faecal but had TMA values that ranged from 3.88 to 17.2.

These observations indicate that ungutted fish may spoil with relatively low TMA values, but that this is not always the case. This is much the same as was observed with bilgy fish (McLean and Castell, 1956).

SOFT FILLETS. When fish are being graded for quality, one of the criteria used is the softness of the muscle. In examining the round or gutted fish, the grader attempts to estimate the degree of softness in the flesh by pressing on it with his finger tips. Muscle of good quality is firm and resilient and should leave no impression where the pressure has been applied. Something similar obtains in the organoleptic grading of fillets, where changes in texture can be seen as well as felt.

There are at least three principal types of softness encountered in commercial cod and haddock fillets. The first is a type of softness that can best be described as "mushy". This develops during the later stages of ordinary bacterial spoilage. Most fish that have developed strong spoilage odours have soft-textured fillets. (Early stages in the development of bilgy fish are often exceptions to this.)

There is a second, quite different type of softness, known to the trade as "slinky" fish. This has nothing to do with bacterial breakdown of the tissue as in "normal" spoilage. It can be observed in fillets freshly cut from recently caught fish. The whole fillet gives the impression of having a jelly-like consistency. It is usually more chalky white and less translucent than normal tissue. It does not readily flake apart. Most commercial fish packers discard these fillets in the cutting line with the explanation that they are "spent" fish. So far we have not been able to identify this type of softness by examination of the whole or gutted fish.

The third and most important texture defect is commonly described as "summer softness". Its chief characteristic is the ease with which the fillets flake apart. If such fillets are suspended by one end, they soon fall apart under their own weight. In a more advanced state the fillets also become "mushy" or

"putty-like". This "summer softness", as the name implies, occurs mainly during the warm summer months of late June through early September. As the fall season progresses, it gradually disappears and rarely occurs during the late fall, winter, and early spring. Although it occurs with both cod and haddock, the latter are the most seriously affected. It is also more prevalent in fish from certain fishing grounds than in others. Trap-caught shore fish are notoriously soft during the summer season. Fish caught in the Gulf of St. Lawrence are much softer than corresponding fish caught on the deep-sea banks. Some fish processors will not cut haddock for their fresh fillet trade if they have been caught in the gulf water during the warm summer season. Others make a point of leaving the skin on the fillets to help hold them together.

All the causal factors for summer softness are not yet thoroughly appraised or understood. It is known to occur chiefly where fish are taken from relatively warm waters. There is experimental evidence to indicate that allowing the fish to encounter unduly high temperatures immediately after being caught will greatly intensify the softness. And there are some observations suggesting that feeding habits of the fish may be a contributing factor. Fish that have been gorging themselves on capelin are often extremely soft-textured. It is also believed that the weakened condition of the fish following spawning is a factor.

Quite apart from the nature and cause of these texture defects, they seriously complicate the problem of grading fresh fish for quality. This is particularly true of summer softness. During July and August, graders inspecting fish from the gulf area and from certain shore fisheries are frequently confronted with haddock that have the appearance of being grade I quality, but which produce fillets so soft that they must be graded II and occasionally relegated to the meal plant. Quite frequently these soft-textured fish produce fillets that show no spoilage odours and have relatively low TMA values.

DISCUSSION

The information presented in this paper shows that the grades given to whole or gutted cod and haddock bear a fairly close relation to the grades given to the fillets cut from the fish. It also shows that when the fish are relatively fresh, the graders tend to slightly down-grade the fillets in comparison with the grades given to the whole fish. As spoilage progresses further, this trend is reversed and they tend to up-grade the fillets in comparison with the grades given to the corresponding whole fish.

The TMA level where this change in the relative severity in grading whole fish and fillets occurs is in the neighbourhood of 1.0 to 1.5. This means, in terms of the Canadian Government's proposed grading scheme, that the graders are likely to show a tendency to underestimate the quality of fillets cut from grade I whole fish; and conversely, they are likely to find acceptable some of fillets cut from fish graded III as whole fish, particularly in the lower TMA ranges (5 to 8).

It has also been shown in this paper that in certain specific types of spoilage the relation between quality of cod and haddock fillets and their TMA values loses its significance. This is the case with fillets cut from bilgy fish, from "feedy"

fish retaining portions of the intestine after gutting, from some ungutted fish and from fish that deteriorate through softness not accompanied by "normal" spoilage.

From a practical viewpoint these results suggest two important questions, the first of which was discussed in the introduction. If there is a slight difference in the grades given to fish muscle, as judged by the grades given to the whole fish and fillet, which is the truest measure of its quality? At least when the fish are in the early stages of spoilage, the evidence points to the whole-fish grading as the most accurate: (a) More spoilage indications are available to the grader in the case of the whole fish; this is especially important when the graders are basing their judgments principally upon what they can see. (b) When visual data are supplemented by careful attention to spoilage odours, the grade given to the fillet more closely approximates the grade given to the whole fish. (c) A considerable amount of evidence has been accumulated showing that, with specific exceptions, there is a close correlation between increasing deterioration and the rise in TMA values. During the earlier stages of spoilage the increase in TMA more closely correlates to the grades given to the whole fish. In any case, it is unlikely that the slight differences that do exist will have a significant effect on commercial grading. At the present stage the chief value appears to be in knowing that such differences do exist.

The second question is concerned with the spoiled or spoiling fish with low TMA values. It has been suggested that TMA values for cod and haddock might have a very useful purpose as an objective measure of spoilage in supplementing or supporting an organoleptic system of grading fish (Castell *et al.*, 1958). How seriously, then, will these obvious exceptions limit the use of TMA values as a supplementary objective measure of spoilage in a system of grading these fish? We now know that such exceptions do exist; it is also known that they are limited to specific types of spoilage, and that these occur under defined conditions. In actual practice the chief use of TMA values will be to assist in the initial training of graders. It will give them a point of reference for their initial judgements of quality. Later it can be used as a check on the efficiency of the graders working under field conditions. Some objective measure must be available so that those in control of the grading program can know how well the various members of their staff are grading fish. Lastly, where any serious argument arises, TMA values may be used as a direct supplement to the graders' judgement based on the organoleptic examination of the fish. It is not anticipated that TMA will ever be used as a primary method of grading fish on the wharf or in the plant. There must be judgements based on sensory inspection.

It obviously follows from this that TMA values cannot be of help in training inspectors to judge the quality of bilgy fish, fish spoiled through heavy faecal contamination resulting from improperly gutted fish, or to a lesser extent from spoilage of ungutted fish. Not only are these types of spoiling fish relatively few, but they will almost always be immediately obvious to the grader and he will not consider using TMA as a measure of their quality.

CONCLUSIONS

1. The grades given by experienced plant foremen and fresh-fish graders to gutted cod and haddock were similar to the grades given to the corresponding fillets cut from these fish.

2. The results suggest that during the earlier stages of spoilage it is easier for a grader to judge the quality of a fish by examining the whole fish, than by examining a fillet cut from it. This is particularly so when the grader cannot give careful attention to the fillet odours.

3. There is a close correlation between grades given to fillets and their TMA values.

4. There are a few definite exceptions to the usual close correlation between TMA values and the quality of cod and haddock muscle. These are principally bilgy fish and certain types of spoilage occurring in improperly gutted or ungutted fish. Other exceptions are found in fish with soft-textured fillets from causes other than bacterial decomposition.

5. Although it is important for graders to be familiar with these exceptions, it is very unlikely that they will seriously interfere with the practical application of a system of grading cod and haddock based on organoleptic examination and supported by TMA values as objective standards of quality.

The problems associated with "summer softness" are a little more serious to the grader. Here again it is realized that TMA will not measure the quality of the flesh if this soft flaky condition is to be taken into consideration. (And it certainly should! During July and August the most prevalent complaint of fish retailers in Ontario towns and cities concerned the texture rather than the odour or flavour of fresh haddock fillets.)

APPENDIX

Statistical treatment of some of the data. By P. L. Hoogland, Fisheries Research Board of Canada, Technological Station, Halifax, N.S.

The strength of the association between grades of round fish and grades of the corresponding fillets may be expressed, e.g., by Spearman's coefficient of rank correlation. To calculate this, the rank numbers 1, 2, 3, 4 and 5 were assigned to the grades I, I or II, II, II or III, and III respectively. The data of Table I were ranked according to these numbers and the correlation coefficient was calculated using Kendall's (1955) method for series with tied ranks. The values found were $\rho_a = 0.938$ and $\rho_b = 0.980$ which indicated an extremely strong association between the two rankings and hence between the grade of a fish and the grade of its fillets. A similar result was obtained with the data in Table III: $\rho_a = 0.949$, $\rho_b = 0.994$.

The data, used to construct Table II, were subjected to the same type of analysis that has been used in the preceding paper (Hoogland, 1958). The correlation coefficient for the relation between grade and TMA index, i.e. $\log(1 + \text{TMA}$

value), was 0.88 for the round fish and 0.83 for the fillets. Both values are highly significant and confirm the conclusions of the earlier papers of this series.

The product-moment correlation coefficients were also calculated for the data of Tables VI and VII. The values found were 0.70 and 0.29 respectively. The first is highly significant and demonstrated the strong association between the grades of the fish in this group and their TMA indices. For the second group of fish, however, the coefficient was only barely significant at the 0.05 probability level and not significant at the 0.02 probability level. Hence, for this group of fish, the existence of a relation between grade and TMA index was very doubtful and if it existed, it could not be very strict. This confirms the conclusion that the relation between grade and TMA value does not hold for fish which spoil under the described conditions.

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A Method of Estimating Natural and Fishing Mortalities[1]

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ABSTRACT

A simple method of estimating instantaneous natural and fishing mortality rates is given. It uses the maximum of the available information. The method requires data on numbers caught by age-classes, and data on (effective) effort for a series of years. For each year-class is calculated the weighted sum of catches from all age-groups from a given age on, and these sums are used as estimates of year-class strengths. The weighting factors depend on the instantaneous fishing and natural mortality rates; the best values of mortality rates are arrived at by iteration. When statistics are not complete a correction factor can be applied. This method is compared with Fry's "virtual" population size estimates; in both cases the basic statistics are catches. We have, however, introduced correction factors to allow for varying fishing intensities and incomplete statistics at older ages.

INTRODUCTION

The most commonly used measure of the survival rate in a fish population is the ratio of the index of abundance of a year-class one year to the index for the next year. From a number of estimates of the survival rate at different levels of fishing the (instantaneous) natural and fishing mortality rates can be obtained by a method described by Beverton and Holt (1954, 1956). Roughly speaking, the method amounts to plotting the total instantaneous mortality rates, as determined from the survival rates, against the effective effort[2] and then fitting a regression line to the points.[3] The total instantaneous mortality rate when the effort is nil, as extrapolated from the regression line, is then the estimated instantaneous natural mortality rate. The instantaneous fishing mortality rate at any point is obtained by multiplying the slope of the line by the effort.

When there is no good index for the effective effort and when the vulnerability fluctuates considerably from year to year, there may be considerable error involved in such estimates. To avoid marked effects of changes in the vulnerability, Fry (1949) has used "virtual" population estimates in place of indices of abundance. He defines a virtual population estimate of a year-class at a given age as the total contribution of the year-class in numbers to the fishery in subsequent years.

Virtual population size estimates of a year-class depend not only on the year-class abundance but also on the effort expended on the year-class, on its vulnerability and on mortalities due to natural causes. Such estimates of two year-classes are close to being comparable indices of abundance only when the

[1]Received for publication November 25, 1957.

[2]By effective effort we mean an index derived from the statistics on effort which is linearly related to the fishing mortality.

[3]We are ignoring a correction factor to account for the effect that the survival rates are usually based on average, annual indices of abundance. To take the correction into account an iterative procedure must be applied.

J. Fish. Res. Bd. Canada, **15**(4), pp. 749–758, 1958.
Printed in Canada.

fishing intensity, the vulnerability and the natural mortalities have been the same during the years of largest contributions of the year-classes to the estimates. For this reason virtual population size estimates cannot be used to determine natural mortality, as calculation of the latter requires considerable fluctuation in fishing intensity. However, the idea as such is useful and we shall indicate how, with an almost obvious modification, we may obtain correct estimates of the size of a year-class if the fishing and natural mortalities are known. Usually we do not know these mortalities, but since the estimates of the size of a year-class at successive ages determine the total mortalities at those ages, we can use this set of circumstances to arrive by the iterative method at values for natural and fishing mortalities, providing that data exist for several year-classes and that fishing intensity has varied over a wide enough range for its effect to be measured. The method will work even if we have data on only two age-groups over a series of years, and it can be used to replace the Beverton and Holt type of estimate of the mortality rates. It has the advantage that it employs the observational data more efficienctly.

PROCEDURE

In the following we shall assume data on catches at each age from several year-classes. To save one subscript which, for the sake of exactness, should be used to separate different year-classes, we shall first consider one year-class only and derive the formula for its size at successive ages. This formula can then be applied to all year-classes considered.

With reference to one year-class, we now denote by:

N_i number of the i-year-old fish at the start of the year

C_i catch in numbers of the i-year-old fish

f_i total effective fishing effort expended on the i-year-old fish

q_i coefficient expressing the fraction of the i-year-old fish caught by one unit of (effective) effort; q_i will be referred to as the catchability coefficient

M_i instantaneous natural mortality rate of the i-year-old fish

$F_i = q_i f_i$ instantaneous fishing mortality rate of the i-year-old fish

$Z_i = F_i + M_i$ total instantaneous mortality rate of the i-year-old fish.

The catchability coefficient, q_i, in the above could be assumed to vary not only with age but also with effort and with changing hydrographic conditions. In these cases we should have to have additional information about its dependence on effort or on hydrographic conditions. We leave, however, these possibilities as special cases and shall not consider them here. We assume, in other words, that q_i is the same at corresponding ages for all year-classes. A similar assumption has to be made for M_i. It will be shown later that we also have to assume that q_i and M_i are the same at least for the two oldest age-groups considered or fulfil some other similar condition.

The catch may now be expressed by the following well-known formula:

$$C_i = \frac{F_i}{F_i + M_i} N_i [1 - \exp - (F_i + M_i)] \tag{1}$$

[4] We write $e^{-x} = \exp - x$.

Because:

$$N_{i+1} = N_i \exp -(F_i + M_i) \tag{2}$$

equation (1) may also be written:

$$C_i = \frac{F_i}{F_i + M_i}(N_i - N_{i+1})$$

Hence:

$$\frac{F_i + M_i}{F_i} C_i = N_i - N_{i+1}$$

Denote:

$$\frac{F_i + M_i}{F_i} = a_i \tag{3}$$

then:

$$a_i C_i = N_i - N_{i+1} \tag{4}$$

The symbol a_i represents the inverse of the fraction of total fish deaths which resulted from capture.

Suppose now that we want to estimate the size of the year-class at the beginning of the year when it is i_λ years old. Suppose further that n specifies the oldest age considered. By summing the terms (4) from the age i_λ to the age n we obtain:

$$\Sigma a_i C_i = N_{i_\lambda} - N_{n+1} \tag{5}$$

where in the summation i ranges from i_λ to n. If the year-class has been fished to extinction, so that $N_{n+1} = 0$, then:

$$\Sigma a_i C_i = N_{i_\lambda} \tag{6}$$

i.e., if we take the weighted sum of catches from the age i_λ onward, we get an estimate of the size of the year-class at the beginning of age i_λ.

If we cannot assume that $N_{n+1} = 0$, i.e., if we study the year-class before it has become extinct, then, as in (2), we have:

$$N_{n+1} = N_{i_\lambda} \exp -\Sigma(F_i + M_i)$$

where i ranges from i_λ to n. If this is substituted in (5) we get:

$$\Sigma a_i C_i = N_{i_\lambda}[1 - \exp -\Sigma(F_i + M_i)]$$

and consequently:

$$\frac{\Sigma a_i C_i}{[1 - \exp -\Sigma(F_i + M_i)]} = N_{i_\lambda}. \tag{7}$$

In this case to obtain the estimated size of a year-class at the i_λth birthday, we divide the weighted sum of catches, $\Sigma a_i C_i$, by the expression in the square brackets. This term is close to 1 if we have several years' data, and is 1 (for

all practical purposes) if the year-class has disappeared from the fishery, i.e., if $N_n = 0$.

An expression alternative to (7) for the size of the year-class may be obtained by writing (5) as follows:

$$\Sigma a_i C_i + N_{n+1} = N_{i_\lambda} \tag{8}$$

where N_n is obtained from (7). In other words, if we take the weighted sum of catches to give the total deaths and add to this sum the estimated number of fish still alive, we obtain an estimate of the size of the year-class at the i_λth birthday. This last expression closely resembles Fry's original idea which was to sum the total catches and add to that sum the estimated number of fish still in the water.

The ratio of the abundance of a year-class at the start of two successive years of its life is the survival rate for the period in question. The natural logarithm of the ratio (with sign changed) is the instantaneous total mortality rate, Z_i. The latter is the sum of the instantaneous fishing and natural mortality rates, and we have:

$$-\log_e \frac{(N_{i+1})}{N_i} = q_i f_i + M_i \tag{9}$$

To obtain estimates of the size of the year-class at the start of two successive years, i.e., N_{i_λ}, $N_{i_\lambda+1}$, we have to know the total catches from the year-class for a number of years, along with estimates of q_i and M_i and the total effort for each year and age. Usually the total catch and total effort, i.e., C_i and f_i, are the only known variables and the values of the catchability coefficient q_i and of the instantaneous natural mortality rate M_i have to be obtained by iteration. This requires at least two years' data for each year-class considered, and at least two different survival rates for each age related to a difference in total effort. Furthermore, some restrictions have to be placed on q_i and M_i as the system does not yield solutions for q_i and M_i for every age-group considered. To be more specific, we cannot estimate q_i and M_i for the oldest age-group considered. Such estimation requires an estimate of the size of the year-class at the beginning and at the end of the oldest age, and the size at the end of the year can hardly be estimated without the following year's statistics. To circumvent this difficulty we may assume that the catchability coefficient, q_i, and the natural mortality, M_i, are the same for at least the two oldest age-groups considered.

Let it be noted that we always face this problem, regardless of the method used, whenever we attempt to calculate mortalities for each age.[5] Usually, however, to attempt to estimate q_i's and M_i's separately for each age is impractical, anyway, because of the variability and inaccuracy of the data.

[5]Beverton and Holt (1954, 1956) write:

$$-\log\left[\frac{C_{i+1}/f_{i+1}}{C_i/f_i}\right] + \log\left[\frac{(qf_i + M)(1 - \exp - (qf_{i+1} + M)}{(qf_{i+1} + M)(1 - \exp - (qf_i + M)}\right] = qf_i + M.$$

This assumes that both M and q are the same at age i and $i + 1$. Should we want the estimates of M and q separately at each age we could release this condition by replacing M and q in the above by M_i and M_{i+1} and by q_i and q_{i+1} respectively. Needless to say, in most cases this would require too much from the data.

Suppose we have data concerning several year-classes. The first step in estimating the q_i's and M_i's is to get initial estimates of the sizes of all year-classes at the start of two or more successive years which bracket the oldest age or ages for which we want to estimate q and M. The initial estimates may be obtained by substituting crude estimates of q and M in (7) or in (8). If we wish to estimate mortalities first at age 9, say, and we have statistics, while not very accurate, up to, say, age 15, we could use virtual population sizes as determined by Fry (1949). This would amount to assuming that the natural mortalities are zero. If, however, we could guess closer to the true value or values than this, we should save effort in subsequent iterations.

Once having obtained the initial trial values of the sizes of the year-classes at the start of the successive years of interest we may substitute them in (9) to obtain the first approximations of $Z_i = q_i f + M_i$. These are then used to calculate the regression line of Z_i on f, where i ranges over the age or the ages considered and f is the measure of effort during any particular year. The slope of this line is a new estimate of q_i, and the Y-intercept at zero effort is a new estimate of M_i. From these, new values of a_i are calculated and substituted along with the new q and M in (7) and (8) to give improved estimates of year-class sizes, N. This procedure is continued until we obtain the values of q and M to which they converge. These give us our best estimates of year-class sizes, N, at each of the ages considered. We may then take the N's for the youngest age-group used in the calculations (or the figures obtained in deriving them, depending on whether we use the formulae (7) and (8) or (7)) and use it in the subsequent iterations to arrive at estimates of q, M, and N for successively earlier ages.

The rapidity of the convergence depends greatly on the goodness of the fit of the (final) regression of total mortality, Z_i, on effort, f. If the scatter around the line is small the convergence is usually rapid; if the scatter is large, the convergence is slower. In the case when the regression of total mortality, Z_i, on f is non-significant, it is possible that the iteration will not converge at all. A good initial choice of q and M reduces the calculations by one or two iterations.

Some measure of the accuracy to which the q_i's and M_i's are estimated can be obtained from the final least square fitting of the regression line using the variances of the intercept and slope.

EXAMPLE

For purposes of illustration we shall use Fry's statistics on the Lake Opeongo trout fishery (1949). Table I is obtained from Fry's Tables I and II. It gives estimates of total numbers of trout caught by year-class and age for 9-year-old or older fish, from 1936 to 1947, and effort expended (in hundred boat-hours) in those years.

We shall calculate q and M at ages 9 and 10, first using statistics on catches of 9-year-old or older fish, and secondly using statistics only on catches of 9- and 10-year-old fish. The results of the latter calculations are then compared with those arrived at by the method of Beverton and Holt. All the calculations have

TABLE I. Estimated number of fish caught in the Lake Opeongo lake trout fishery, from Fry (1949), and fishing effort in hundreds of boat-hours. The top diagonal line represents 9-year-old fish, and the second diagonal 10-year-old fish, and so on.

Year of capture	Number of trout caught at each age, by year-classes											Effort f_i
	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937	
1936	478	...	...	...	...	...	...	...	...	...	...	20.3
1937	176	555	...	...	...	...	...	...	...	...	...	22.4
1938	3	90	195	...	...	...	...	...	...	...	...	16.3
1939	24	47	90	223	...	...	...	...	...	...	...	13.8
1940	0	6	14	46	120	...	...	...	...	...	...	11.7
1941	0	11	11	11	22	104	...	...	...	...	...	11.3
1942	0	2	2	9	8	28	53	...	...	...	...	5.7
1943	0	0	0	6	24	0	42	133	...	...	...	7.1
1944	4	4	9	22	9	31	44	93	198	...	...	9.2
1945	0	16	37	16	43	21	37	84	159	373	...	14.0
1946	0	0	4	7	0	7	11	26	47	93	217	17.4
1947	0	0	0	3	3	6	0	3	12	18	76	12.3

been carried out using first formula (7) and then using formulae (7) and (8). Since, in the examples worked out, the results came to about the same, and since the method using both formulae (7) and (8) is far more expedient to use, only the latter calculations will be shown in detail.

COMPUTATION USING DATA FOR ALL AGES FROM AGE 9. Let us first consider the situation when we use all statistics from age 9 onward. We shall assume that q and M are the same at all ages considered; should a more refined study be necessary we could assume, e.g., that q and M are the same for all ages from age 10 on but not necessarily at age 9.

To get the iteration started we take, quite roughly, an average survival rate of 60% for 9- and 10-year-old fish which gives an instantaneous mortality rate of 0.55. From this we assume, again quite arbitrarily, that 0.45 is due to fishing and 0.10 is due to natural causes. The 0.45 fishing mortality corresponds with an average effort from 1936–47 of 15 hundred boat-hours. Thus, for $M = 0.10$ a reasonable approximation of q is $q = 0.03$ ($15 \times 03 = 0.45$). These values of q and M are taken as initial values for 9-year-old or older fish.

Table II shows in detail the calculations necessary for one iteration. Columns 2 and 3 give the instantaneous fishing and total mortalities corresponding to the initial values $q = 0.03$ and $M = 0.10$. Since statistics are complete up to 1947, the total mortality rates are accumulated beginning that year in Column 4. Corresponding values of $[1 - \exp - \Sigma(F+M)]$ are then taken from an appropriate table and tabulated in Column 5 (cf. formula 7). The values of a_i (Column 6; cf. formula 3) are derived by dividing the total mortality rate (Column 3) by the fishing mortality rate (Column 2). The summation, $\Sigma a_i C_i$, in Column 8 is obtained separately for each year-class by multiplying the a_i of any particular year with the same year's catch of whatever age it may be, and totalling these cross products up to age 10; thus for the first figure in Column 8 we have $241.2 = (1.3571 \times 4) + (1.4762 \times 0) + (1.5882 \times 0) + (1.2941 \times 0) + (1.2857 \times 0) + (1.2439 \times 24) + (1.2041 \times 3) + (1.1493 \times 176)$, and similarly for all the other figures. To obtain the first estimates of the year-class size at age 10, the weighted

TABLE II. Calculations required to arrive at year class size estimates and at total instantaneous mortality rates.

1	2	3	4	5	6	7	8	9	10	11	12	13
Year	$F=qf$	$F+M$	$\Sigma(F+M)$	$1-\exp-\Sigma(F+M)$	a_i	Year-class	$\Sigma a_i C_i$ $(i \leqslant 10)$	$\frac{\Sigma a_i C_i}{1-\exp-\Sigma(F+M)}$	Year-class	$\frac{a_9 C_9 + \Sigma a_i C_i}{1-\exp-\Sigma(F+M)}$	Survival at age 9	$Z = -\log_e(N_{10}/N_9)$
1936	0.61	0.71	6.04	0.9976	1.1639	...	...	...	1927	798.7	0.303	1.19
1937	0.67	0.77	5.33	0.9952	1.1493	1927	241.2	242.4	1928	857.4	0.256	1.36
1938	0.49	0.59	4.56	0.9895	1.2041	1928	217.2	219.5	1929	449.0	0.477	0.74
1939	0.41	0.51	3.97	0.9811	1.2439	1929	210.2	214.2	1930	440.9	0.371	0.99
1940	0.35	0.45	3.46	0.9686	1.2857	1930	158.4	163.5	1931	307.1	0.498	0.70
1941	0.34	0.44	3.01	0.9550	1.2941	1931	145.9	152.8	1932	273.7	0.508	0.68
1942	0.17	0.27	2.57	0.9235	1.5882	1932	128.5	139.1	1933	285.0	0.704	0.35
1943	0.21	0.31	2.30	0.8997	1.4762	1933	180.6	200.7	1934	503.3	0.610	0.49
1944	0.28	0.38	1.99	0.8633	1.3571	1934	265.0	307.0	1935	603.8	0.555	0.59
1945	0.42	0.52	1.61	0.8001	1.2381	1935	268.1	335.1	1936	663.9	0.304	1.19
1946	0.52	0.62	1.09	0.6638	1.1923	1936	133.7	201.4	1937	516.1	0.499	0.70
1947	0.37	0.47	0.47	0.3750	1.2703	1937	96.5	257.3	...	...	...	...

sum of catches (Column 8) is divided by the values of $[1-\exp-\Sigma(F+M)]$ (Column 5; cf. formula 7) and tabulated in Column 9. To the year-class size at age 10 (Column 9) we have added the catch at age 9 weighted by the a_t corresponding to the year to arrive at the first estimates of the year-class size at age 9, Column 11. Here we have used formula (8). Thus the first figure in Column 11 is $798.7 = 242.4+(1.1639\times478)$. The ratio of the number of 9-year-old fish to that of 10-year-old fish taken separately for each year-class gives the survival rate at age 9 (Column 12) and the natural logarithms of the survival rates give the total mortality rates (Column 13).

The regression line of the first estimates of the total instantaneous mortality rates (Column 13 of Table II) is then calculated. This gives a slope $q = 0.051$ and the Y-intercept $M = 0.124$. These values are then taken as new estimates of q and M (replacing $q = 0.03$ and $M = 0.10$), and exactly the same procedure as that in Table II is repeated. All in all, four iterations have been done, and the resulting total mortality rates along with M and q are tabulated in Table III.[5]

TABLE III. Total instantaneous mortality rates, Z, and resulting values of q and M for successive iterations using all data from age 9 on.

Year	Second iteration	Third iteration	Fourth iteration
	Z	Z	Z
1936	1.20	1.20	1.20
1937	1.38	1.37	1.37
1938	0.76	0.75	0.75
1939	1.02	1.02	1.01
1940	0.72	0.71	0.72
1941	0.72	0.71	0.71
1942	0.36	0.37	0.38
1943	0.52	0.53	0.54
1944	0.65	0.66	0.66
1945	1.34	1.37	1.37
1946	0.89	0.91	0.91
M	0.1550	0.1671	0.1671
q	0.0526	0.0520	0.0520

The final figures $q = 0.052$ and $M = 0.167$ have standard deviations of 0.012 and 0.175 respectively. The correlation coefficient $r_{Z,f}$ between the total instantaneous mortality rates at age 9 and effort is 0.815.[6]

COMPUTATION USING DATA FOR AGES 9 AND 10 ONLY. To arrive at the values of q and M using statistics on catches only at ages 9 and 10, calculations similar to those in Table II are carried out. The only difference is that to obtain estimates of the year-class size at age 9 the sum of total mortalities and the weighted sum of catches both contain one term only. Thus in Table II Columns 3 and 4 would be equal and Column 8 would be obtained by multiplying the catch at age 10 with the appropriate a_t.

[6] If formula (7) is used exclusively then we get $q = 0.052$, $M = 0.185$, $s_q = 0.012$, $s_M = 0.179$ and $r_{Z,f} = 0.811$. These values are about the same as those obtained when using formulae (7) and (8).

Starting with $q = 0.03$ and $M = 0.10$, the total instantaneous mortality rates are obtained as tabulated in Table IV. From these the new q and M are calculated for the second iteration and so on. Six iterations were necessary to arrive at the final values $q = 0.044$ and $M = 0.446$ and with standard deviations $s_q = 0.017$ and $s_M = 0.247$. The correlation coefficient is $r_{Z,f} = 0.644$.[7]

TABLE IV. Total instantaneous mortality rates, Z, and resulting values of q and M for successive iterations using data at ages 9 and 10 only.

Year	First iteration	Second iteration	Third iteration	Fourth iteration	Fifth iteration	Sixth iteration
	Z	Z	Z	Z	Z	Z
1936	0.91	1.06	1.11	1.13	1.14	1.14
1937	1.29	1.49	1.56	1.56	1.57	1.57
1938	0.61	0.76	0.81	0.83	0.84	0.84
1939	0.99	1.16	1.28	1.31	1.32	1.32
1940	1.07	1.29	1.39	1.44	1.44	1.45
1941	0.54	0.71	0.78	0.80	0.81	0.82
1942	0.31	0.41	0.49	0.54	0.56	0.57
1943	0.40	0.51	0.58	0.64	0.66	0.66
1944	0.44	0.56	0.62	0.66	0.68	0.69
1945	1.07	1.26	1.34	1.38	1.39	1.40
1946	0.70	0.89	0.92	0.93	0.93	0.94
q	0.0448	0.0492	0.0455	0.0447	0.0439	0.0435
M	0.1492	0.2501	0.3718	0.4135	0.4349	0.4460

[7]When formula (7) is used exclusively we obtain $q = 0.046$, $M = 0.408$, $s_M = 0.280$, $s_q = 0.019$ and $r_{Z,f} = 0.618$. These agree closely with the results obtained when applying both formulae (7) and (8).

COMPARISON WITH BEVERTON AND HOLT'S METHOD. For the sake of comparison we have also applied the Beverton and Holt method to the data. Catches per unit of effort on which figures we have based our calculations are given in Table V.[8] The results are $q = 0.047$, $M = 0.374$, $s_q = 0.026$, $s_M = 0.380$ and $r_{Z,f} = 0.513$.

TABLE V. Catches per unit effort (i.e., per hundred boat-hours) of 9- and 10-year-old fish as obtained from Table I.

Year of capture	Catch per unit effort	
	9-year-olds	10-year-olds
1936	23.5	...
1937	24.8	7.9
1938	12.0	5.5
1939	16.2	6.5
1940	10.3	3.9
1941	9.2	1.9
1942	9.3	4.9
1943	18.7	5.9
1944	21.5	10.1
1945	26.6	11.4
1946	12.5	5.3
1947	...	6.2

[8]Beverton (1954) has applied this method to Fry's data with somewhat different results. We have, however, used one more year's data, and also catches per unit effort obtained from Table I are not always the same as those in the table on page 117 of Beverton (1954). This inconsistency goes back to the original data in Fry (1949).

It is worth while to summarize by noting that in the example worked out the correlation coefficient $r_{Z,f}$ between the total instantaneous mortality rate at age 9 and effort is 0.815 when all available data is used and is 0.644 when data on catches only at ages 9 and 10 are used. The corresponding value of $r_{Z,f}$ when the Beverton and Holt method is applied was calculated to be 0.513. The increase in the amount of information used appears to bring about a remarkable increase in the accuracy of estimation.

ACKNOWLEDGMENTS

I am very much obliged to Drs. L. M. Dickie, F. E. J. Fry and W. E. Ricker for their useful suggestions and editorial comments. I also wish to thank Messrs. R. J. H. Beverton and S. J. Holt who read the earlier version of the manuscript. I should like to note that this paper is a direct result of stimulating discussions at the Joint Scientific Meeting of the International Commission of Northwest Atlantic Fisheries, the International Council for the Exploration of the Sea, and the Food and Agricultural Organization of the United Nations, held in Lisbon May 27 to June 3, 1957.

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